Angiosperm family pairs: preliminary phylogenetic analyses

WALTER S. JUDD
Department of Botany, 220 Bartram Hall,
University of Florida, Gainesville, FL 32611-8526

ROGER W. SANDERS
Fairchild Tropical Garden, 11935 Old Cutler Road,
Miami, FL 33156; current address: Botanical Research
Institute of Texas, 509 Pecan Street, Fort Worth, TX 76102

MICHAEL J. DONOGHUE
Department of Organismic and Evolutionary Biology,
Harvard University, Cambridge, MA 02138

Abstract: We report a series of phylogenetic analyses of selected taxa from several presumably closely related groups of angiosperm families, i.e., Apocynaceae/Asclepiadaceae, Araliaceae/Apiaceae, Capparaceae/Brassicaceae, Caprifoliaceae/Dipsacaceae/Valerianaceae, Moraceae/Urticaceae, and Sapindaceae/Aceraceae/Hippocastanaceae. These studies lead to the conclusion that Apocynaceae, Araliaceae, Capparaceae, Caprifoliaceae, Moraceae, and Sapindaceae are paraphyletic, with the related families nested within them. Studies within Fabales, Papaverales, Lamiales, and several other groups of families, indicate a similar pattern. In most of these cases the paraphyletic group is best developed in the tropics, with groups that are more widespread in temperate regions evolving later. With a few exceptions, members of the paraphyletic group are mostly woody plants, while members of the derived temperate lines are mostly herbaceous. In general, it appears that the distinctive morphological specializations of the more temperate lines can be traced to related tropical plants. Traditional family circumscriptions are apparently the result of a temperate bias on the part of plant systematists. These do not reflect phylogenetic relationships accurately and will tend to impede progress in understanding the diversification of angiosperms. We recommend a series of taxonomic changes, most of which involve the union of traditionally recognized families, and we provide phylogenetic definitions of the newly circumscribed taxa. We hope that these taxonomic changes will draw attention to the morphological diversity among the tropical relatives of familiar temperate plants, and will help us understand the sequence of events leading to the origin and radiation of temperate groups.

The taxonomic affinities between Apocynaceae and Asclepiadaceae; Araliaceae and Apiaceae; Capparaceae and Brassicaceae; Caprifoliaceae, Dipsacaceae, and Valerianaceae; Moraceae and Urticaceae; and Sapindaceae, Aceraceae, and Hippocastanaceae have been recognized by nearly all modern plant systematists, e.g., Takhtajan (1980), Cronquist (1981), Dahlgren (1983), Thorne (1983, 1992a, 1992b), although a few have differed, e.g., Hutchinson (1969, 1973). It is noteworthy that the first-listed family in each of these pairs (or triads) is mainly tropical, while the second (or second and third) is (are) cosmopolitan to temperate in distribution. An exception is the Caprifoliaceae, which are mainly temperate to warm temperate; even this family, however, is more tropical than the related Dipsacaceae. Despite the general consensus that the families within each of these pairs (or triads) share a common ancestor, few detailed studies exist that address the nature of their phylogenetic (or cladistic) relationship. It has been suggested that the "tropical" member of each of these family groups is paraphyletic and the more temperate family (or families) originated later and is (are) either monophyletic or polyphyletic (Donoghue & Cantino, 1988; Thorne, 1973a, 1983), but this hypothesis has not been explicitly tested (and other views certainly are possible, e.g., the families comprising each pair may be monophyletic and represent sister groups). It is our intent here to perform preliminary cladistic analyses of these family groups in order to explicitly test the proposition that the "tropical" member of each of these family groups is paraphyletic.

Until phylogenetic relationships within each of these groups of families are clarified, it is not possible to address other significant macroevolutionary, historical, or taxonomic questions, such as: 1) Why are the predominantly tropical families more diverse morphologically than their more temperate counterparts? 2) Why are the predominantly temperate families Brassicaceae and Apiaceae richer in species than their more tropical relatives Capparaceae and Araliaceae? 3) What effects have temperate biases had on family circumscriptions? and 4) Are the members of these family groups circumscribed in a non-arbitrary fashion? That is, do currently recognized families accurately reflect genealogy ?

This paper presents the results of preliminary cladistic analyses of the family groups listed above. We make several taxonomic recommendations based on these results. The macroevolutionary implications of our results and their correlation with paleobotanical data are treated in a separate paper (Donoghue, Judd, & Sanders, in prep.).

MATERIALS AND METHODS

Preliminary cladistic analyses of the phylogenetic relationships of selected taxa within each family pair or triad were conducted using the branch-and-bound algorithm (Hendy & Penny, 1982) as implemented in PAUP (i.e., Phylogenetic Analysis Using Parsimony, Version 3.0s, Swofford, 1991). We also used MacClade, Version 3.0 (Maddison & Maddison, 1992) in order to explore alternative tree topologies and to determine character changes along the branches. Genera were used as terminal units in the analyses, and we were careful to include sufficient taxa in each analysis to test the proposition that the "tropical" member of each of these family groups is paraphyletic. Thus, a limited number of exemplar genera from the families of each pair or triad was used. Taxonomic groups suspected of being paraphyletic were sampled more intensively than those for which we had preliminary evidence of monophyly. Our analyses should not be construed as detailed and definitive phylogenetic studies of each of these groups; in fact, we hope that our results will encourage more detailed investigations. The resulting cladograms should be considered tentative because only selected genera were included. They are, nevertheless, useful in providing a concrete starting point for future investigations.

We concentrated on mainly morphological and anatomical taxonomic characters; molecular results, however, are discussed when available. Nearly all characters are based on the authors' observations of specimens deposited in the herbaria cited in the acknowledgements (and, where possible, of living material). Some features are taken only from the literature; these are indicated in the individual analyses, and the pertinent literature is referenced. Characters were polarized using out-group analysis (Stevens, 1980; Farris, 1982; Maddison et al., 1984). One or more outgroups were included in each analysis, and trees were rooted along the branch connecting the outgroup(s) to the ingroup taxa. Outgroups were selected that share higher-level apomorphies with the ingroup taxa, i.e., taxa hypothesized to include the sister group and more distant relatives. Nearly all characters were readily divisible into discrete states, thus avoiding arbitrary decisions relating to state delimitation (see Stevens, 1991). A few taxa are polymorphic for particular characters; in such cases we generally attempted to score the taxon with the condition hypothesized (on other phylogenetic grounds) to be ancestral in that taxon. Details and problems regarding selection of taxa and characters (and character coding) are presented with each analysis. In general, we have been careful to include the range of variability exhibited in the families being discussed. Multistate characters were considered to be unordered unless stated otherwise. Results and discussion of the cladistic analysis for each of the family groups are presented below. Following these, we discuss similar patterns in other family groups, summarize our phylogenetic conclusions, and provide taxonomic recommendations.

APOCYNACEAE AND ASCLEPIADACEAE

Taxa and characters. Nine ingroup taxa were scored for fourteen characters (Tables 1-3). A hypothetical loganiaceous outgroup (see below) was included in the analysis and used to root the results. The Apocynaceae and Asclepiadaceae generally have been included in the Gentianales (Schumann, 1895; Solereder, 1895;

TABLE 1. Apocynaceae/Asclepiadaceae taxa*

Apocynaceae
  Plumerioideae
    Carissa
    Plumeria
    Kopsia
    Thevetia
    Tabernaemontana
  Apocynoideae
    Nerium
Asclepiadaceae
  Periplocoideae
    Cryptostegia
  Asclepiadoideae
    Asclepias
    Matelea
Loganiaceae (OG) or *Plocosperma*

*Classification based on Rosatti (1989)

Wagenitz, 1992), a relationship supported by the possible synapomorphies of colleters on the sepals and/or stipules and leaf bases, alkaloid chemistry, internal phloem, and contorted corolla. The Loganiaceae are the most plesiomorphic of the Gentianales and are presumably paraphyletic because they share no synapomorphies other than those that diagnose the order (Bremer & Struwe, 1992; Chase et al., 1993). On the other hand, the Apocynaceae/ Asclepiadaceae lineage does possess certain potential synapomorphies with *some members* of the Loganiaceae, including: corolla tubular to infundibular and contorted in bud; gynoecium bicarpellate with very late or only partial postgenital fusion of carpels; placenta distended, or massive, bearing small, poorly developed ovules at anthesis; seeds lenticular and umbonate, flattened in a plane tangential to the placenta with the hilum in the center of the inner face; and testa papillate (see also Bremer & Struwe, 1992). Distally distinct ovaries and styles are well known in the loganioid *Mitreola* and *Mitrasacme* (Endress et al., 1983), which are, however, herbs with valvate corollas. However, in *Gelsemium*, which is fully syncarpous at maturity, the distal half of the ovaries and styles remain distinct until the bud is two or three mm long (R.W. Sanders, pers. observations). This condition may be more widespread in the Loganioideae and needs further study.

Thorne (1976) and Tahktajan (1980) consider *Plocosperma* (Loganiaceae, Plocospermoideae) to be transitional to the Apocynaceae. However, of the postulated synapomorphies (listed above) it has only an infundibular, contorted corolla. Its elongate follicle-like capsule and single comose (but linear and basally attached) seed (Solereder, 1895) may be convergences with the Apocynaceae. It is noteworthy, however, that in the preliminary cladistic analysis of Gentianales conducted by Bremer and Struwe (1992), *Plocosperma* was positioned as the sister group of *Nerium* (a representative of Apocynaceae/Asclepiadaceae) on the basis of its follicle-like capsule, comose seed, and parietal placentation. *Plocosperma*, when used as an alternate outgroup, yielded the same cladogram as the generalized loganioid outgroup used here.

The interpretation of gynoecial and androecial characters in the Apocynaceae (see Table 2), follows the work of Fallen (1986). Note that the states of character 12 (i.e., style form) are considered to form an ordered linear transformation series. Certain characters, such as corolla shape (tubular vs. rotate), were not included because they vary within subfamilial or tribal groups represented by the selected genera. Certain fruit characters associated with animal dispersal were omitted because the diversity of forms made interpretation of homologies too unreliable.

Results. The branch-and-bound analysis yielded a single 20-step tree without homoplasy, i.e., consistency index (CI) of 1.0 and retention index (RI) of 1.0 (Fig. 1). Two optimizations were equally parsimonious for the unordered states of the translator structure (char. 9). There is no reason for assuming that either condition is the immediate precursor of the other. If the translator types form a linear transformation series (as shown in Fig. 1), there is no autapomorphy for *Cryptostegia* and, hence, no character support for the monophyly of the periplocoid clade. The opposite is true, however, if the apomorphic states of the translator were derived separately.

When all multistate state characters are treated as unordered, analyses yielded two 20-step trees, with more than one optimization for

TABLE 2. Apocynaceae/Asclepiadaceae Characters

1. Latex: absent (0), present (1)
2. Filaments: distinct (0), connate (1)
3. Filaments: simple (0), abaxial appendages (1)
4. Anther sacs: 4 (0), 2 (1)
5. Anthers: distant (0), connivent (1), strongly adpressed (2)
6. Anthers: free (0), adherent and weakly adnate to style-head by intertwining trichomes and glutinous secretions (i.e., viscin; Fallen, 1986) (1), strongly adnate by solid parenchymatous tissue (2)
7. Anthers: fully fertile, lacking sclerenchyma, bases not sagittate (0), fertile only distally, other parts with sclerenchyma, bases sagittate (1)
8. Connective: lacking apical appendage (0), with apical appendage (1)
9. Translator (structure bearing pollen from thecae of adjacent anthers): lacking (0), blade- or cup-like, composed of hardened, exfoliating, adnate adaxial walls of thecae, corpusculum basal (1), yoke-like, composed of hardened resinous secretions, proximally attached to pollen masses from thecae, corpusculum apical (2)
10. Pollen: shed as monads, loosely coherent by means of viscin (0), shed in tetrads, these loosely coherent (1), shed in tetrads, strongly coherent in hardened masses (true pollinia; Safwat, 1962) (2)
11. Ovaries: syncarpous, placentation axile or parietal (0), apocarpous, placentation marginal (fruit a follicle or derived type) (1)
12. Style: not distally enlarged (0), clavate or fusiform below style branches (i.e., development of a style-head), enlarged area latitudinally uniform (1), style head an abruptly enlarged and latitudinally zonate region (2), style head as in state 2, but interrupted along 5 radii (more or less pentagonal) (3) (ordered)
13. Viscin secretions of gynoecium: absent (0), present (1)
14. Testa: marginally ridged or winged (0), distally comose (i.e., wing deeply divided into fine bristles) (1)

characters 6, 9, 10, and 12. The topology of the first tree is identical to Figure 1, while the second tree contains a trichotomy involving *Plumeria*, *Kopsia*, and the *Thevetia*-to-*Matelea* clade. The combinable component (or "semi-strict") consensus tree (Bremer, 1990) is identical to the single tree discovered in the first analysis (Fig. 1).

The Apocynaceae plus Asclepiadaceae form a monophyletic group differing from their loganioid relatives by the presence of latex (char. 1), the distinctive style-head (char. 12), and the glutinous secretion (viscin) of the style (char. 13). A basal branch includes *Carissa* (Plumerioideae, Carisseae), which lacks the additional synapomorphies of connivent anthers (char. 5) and apocarpous ovaries with marginal placentation that develop into follicles or follicle-derived fruits (char. 11). Fallen (1986) has shown that the Carisseae are congenitally syncarpous, and this character may be a retained plesiomorphy. However, if late postgenital syncarpy is the rule in the loganioid outgroup, the carissoid condition would be an autapomorphy.

The remaining genera (each representing a separate tribe or subfamily) exhibit a stepwise accumulation of androecial and gynoecial characters that are associated with increased efficiency of the pollination mechanism (Schick 1980, 1982; Kunze, 1982; Fallen, 1986). Included among these innovations are the enlarged, five-sided style-head that is differentiated into zones for pollen deposition, viscin secretion, and pollen reception; apical anther appendages; differentiation of fertile and sclerified sterile portions of the anthers; and the development of adhesive trichome pads on the style-head and/or anthers (Fig. 1). The Asclepiadaceae are further characterized by the development of agglutinated pollen that is transferred en masse by a translator to the receptive style-head site, and by filament appendages (often associated with nectar production). The "pollinium" in *Cryptostegia* (i.e., Periplocoideae) is composed of loosely agglutinated pollen (shed in tetrads) resting on the corneous translator. The sticky appendage that contacts the pollinator (i.e., the corpusculum) is basal. This type of translator

TABLE 3. Apocynaceae/Asclepiadaceae Matrix (* =characters with notes)

						*	*			1	*	*		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4
Loganiaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carissa	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Plumeria	1	0	0	0	1	0	0	0	0	0	1	1	1	0
Kopsia	1	0	0	0	1	0	0	0	0	0	1	2	1	0
Thevetia	1	0	0	0	1	0	0	1	0	0	1	3	1	0
Tabernaemontana	1	0	0	0	1	0	1	1	0	0	1	3	1	0
Nerium	1	0	0	0	1	1	1	1	0	0	1	3	1	1
Cryptostegia	1	0	1	0	2	2	1	1	1	1	1	3	1	1
Asclepias	1	1	1	1	2	2	1	1	2	2	1	3	1	1
Matelea	1	1	1	1	2	2	1	1	2	2	1	3	1	1

6: Observation under 30-power magnification suggests the connection of anthers to style-head in *Cryptostegia* to be solid parenchyma; M. F. Endress (pers. comm.) has confirmed this anatomically. **7:** Anthers in *Cryptostegia* strongly cordate, basal lobes empty of pollen, texture somewhat chartaceous and resistent to tearing; M. F. Endress (pers. comm.) has found sclerenchyma in anatomical studies; these features are interpreted as a modification of state 1. **11:** Placentation axile in most Loganioideae, parietal (shallowly) in *Plocosperma*, axile in *Carissa,* and intruded parietal in other Carisseae. Carpels secondarily nearly syncarpous in *Thevetia*; however, the bicornate endocarp shape implies that the fruit is derived from a pair of follicles. **12:** Outgroup scored as 0; the terminally discoid stigma of *Fagraea* is interpreted as nonhomologous to a style-head. The bifurcate, longitudinally stigmatic style-branches of *Plocosperma* and the Gelsemieae may be ancestral to the clavate style-head via connation and elaboration.

may be either a symplesiomorphy or a synapomorphy in the Periplocoideae (see above). *Asclepias* and *Matelea* (representing Asclepiadoideae) share the loss of two thecae per anther and the agglutination of pollen into a hardened, true pollinium that is attached directly to an apical translator (Fig. 1). This yoke-shaped translator physically separates the two pollinia, and the corpusculum is at the apical point of the translator. A further synapomorphy for the asclepiadoids is the connation of the filaments into a tube around the style.

Discussion. Our results support the monophyly of Asclepiadaceae (including Periplocoideae), in contrast to Wanntorp (1988), who conducted a similar cladistic study. He concluded that the Periplocoideae arose from the Plumerioideae (corresponding in our cladogram to a branch between *Kopsia* and *Thevetia*) and converged toward the Asclepiadoideae in several advanced characters. He coded Periplocoideae differently from the Asclepiadoideae in the following ways: not forming a connivent anther cone, not depositing the pollen on the upper side of the style-head, not having basally sterile, sagittate anthers, not having a pentagonal style-head, and not having the style-head adnate to the anthers by a solid mass of tissue. On the contrary, we found all these conditions to be present in fresh material of *Cryptostegia*. If Wanntorp's hypothesis were correct, there would have to be an independent origin in the Periplocoideae and Asclepiadoideae of all the above features, as well as dorsally appendaged filaments, comose testas, and pollen in tetrads (which were not included in his analysis).

As delimited in several evolutionary classifications (Cronquist, 1981; Dahlgren, 1980; Macfarlane, 1933; Tahktajan, 1980), the Asclepiadaceae (either defined narrowly, or broadly are monophyletic, whereas the Apocynaceae clearly are paraphyletic. As delimited by Thorne (1976, 1983, 1992a, 1992b), the Apocynaceae include the Asclepiadaceae and are, thus, monophyletic.

Justification for maintaining the two families was presented by Cronquist (1981, p. 861): "It has long been customary, and I believe it is

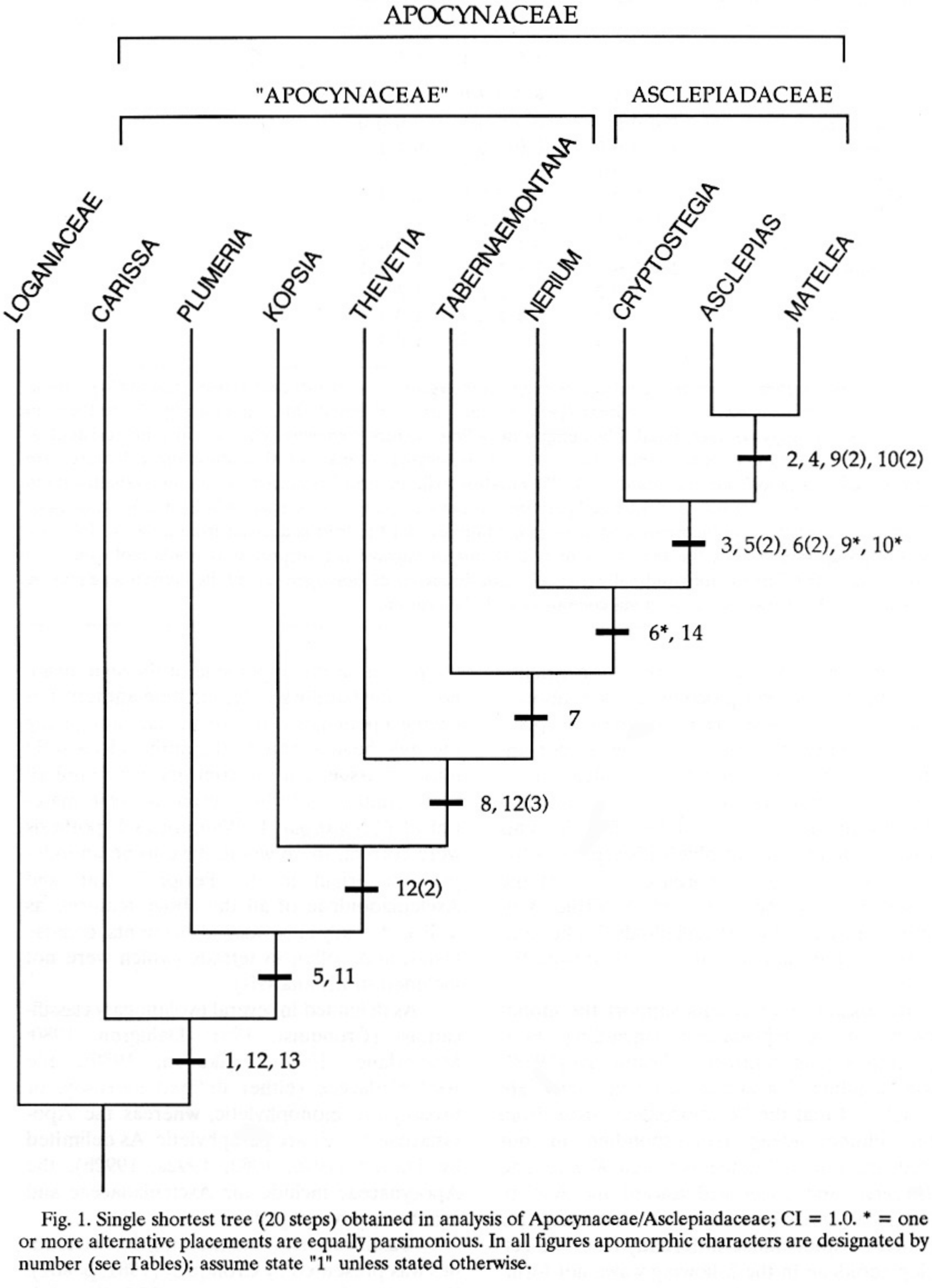

Fig. 1. Single shortest tree (20 steps) obtained in analysis of Apocynaceae/Asclepiadaceae; CI = 1.0. * = one or more alternative placements are equally parsimonious. In all figures apomorphic characters are designated by number (see Tables); assume state "1" unless stated otherwise.

conceptually useful, to recognize just two families in the group. The distinction is drawn on the method of pollination, specifically on the presence of a translator in the Asclepiadaceae and its absence from the Apocynaceae." In contrast, Thorne (1976, p. 91) noted that "Only the inhibiting force of tradition prevents general acceptance of an expanded Apocynaceae." We believe that this tradition stems from a nineteenth-century family concept that depended on a morphological gap between the temperate Apocynaceae and Asclepiadaceae that were known at the time, and perhaps also on the unwieldy size of the undivided family (Stevens, 1993). Based on our analysis, we agree with Thorne that it is no longer desirable to maintain the standard separation between these families, which renders the traditional Apocynaceae paraphyletic. We recommend that the name Apocynaceae be redefined to refer to the most recent common ancestor of plants previously considered to be Apocynaceae and Asclepiadaceae, and all of its descendants (a "node-based" phylogenetic definition; see de Queiroz and Gauthier, 1990).

TABLE 4. Araliaceae/Apiaceae Taxa*

Araliaceae		
		Aralia
		Schefflera
		Dendropanax
		Oreopanax
		Myodocarpus
Apiaceae		
	Apioideae	
		Apium
		Chaerophyllum
	Saniculoideae	
		Eryngium
		Sanicula
	Hydrocotyloideae	
		Hydrocotyle
		Centella
Pittosporaceae		
		Pittosporum (OG)

*Classification according to Cronquist (1981).

ARALIACEAE AND APIACEAE

Taxa and characters. Eleven representative genera of Araliaceae and Apiaceae were scored for eighteen characters (Tables 4-6). Pittosporaceae were included as an outgroup because this family shares the following presumably derived features with the Araliaceae/Apiaceae complex: schizogenous ducts with mucilage, resin, and ethereal oils in the pericycle; details of root anatomy and development, i.e., resin canals located in such a manner that a characteristic arrangement of adventitious roots results; presence of a similar array of distinctive secondary compounds, e.g., falcarinone polyacetylenes, triterpenoid saponins, chlorogenic and quinic acids, ethereal oils; unitegmic and tenuinucellate ovules; tiny embryos; flowers with only 5 stamens; and cataphylls at the base of the seasonal growth unit. A relationship between these families also has been postulated by van Tieghem (1884), Hegnauer (1969), Jay (1969), Gibbs (1974), Dahlgren (1975, 1980, 1983), Crisp and Taylor (1990), Anderberg (1992), and Thorne (1992b). Cronquist (1981, p. 553) noted that "the hypogynous, multiovulate flowers of the Pittosporaceae, with a well developed calyx, are obviously much more primitive than the epigynous, pauciovulate flowers of the Araliales, with reduced calyx." He placed Pittosporaceae in the Rosales (the basal complex within his Rosidae) on the basis of symplesiomorphic features, mainly their generalized 5-merous flowers, and he interpreted their chemical and anatomical similarities with Araliales as parallelisms. In contrast, we consider these characters to be synapomorphic, indicating a genealogical link between Pittosporaceae and Araliaceae/Apiaceae. In any case, the use of a generalized out-group based on characters of Rutales (or Sapindales), as suggested by Cronquist (1968, 1988) and Eyde and Tseng (1971), changed the polarity of only one character (2: leaves simple vs. compound), and had no effect on in-group structure in the resulting cladogram.

The Araliaceae/Apiaceae are genealogically close to the sympetalous Dipsacales and Asterales (incl. Campanulales), all possessing a corolla tube that originates either before or at the same time as the corolla lobes, referred to as early sympetaly by Erbar (1991). As noted by Erbar (1991, p. 443; Erbar & Leins, 1988) the Araliaceae, typically considered to have separate petals, contains members "with

TABLE 5. Araliaceae/Apiaceae Characters

1. HABIT: woody (0), herbaceous (1)
2. LEAVES: simple (0), compound/dissected (1), unifoliate (2)
3. PETIOLES: not sheathing (0), expanded, sheathing at base (1)
4. STIPULES: lacking (0), present (1)
5. INFLORESCENCES: cymose (0), umbellate (1)
6. INFLORESCENCES: not compound umbels (0), compound umbels (1)
7. CALYX: conspicuous (0), reduced, minute (1)
8. PETALS: imbricate (0), valvate (just before anthesis) (1)
9. OVARY: superior (0), inferior (1)
10. CARPELS: more than 2 (0), 2 (1)
11. STYLOPODIUM: absent (0), present (1)
12. STYLOPODIUM: confluent with style (0), separated from style by a groove (1)
13. FRUITS: fleshy, indehiscent (0), dry, schizocarpic (1)
14. VITTAE (schizogenous oil canals): absent (0), present in fruit (1), elongate (2)
15. CARPOPHORE: absent (0), present (1)
16. MERICARPS: not borne at apex of carpophore (0), borne at apex of more or less forked carpophore (1)
17. ENDOCARP: absent (0), present (1), some development (reduced) (2)
18. FRUIT SURFACE: smooth or ribbed (0), scaly or spiny (1)

a corolla initiated as a low ring primordium which, however, does not grow up into a tube," i.e., early sympetaly. A close phylogenetic relationship between the sympetalous Pittosporaceae and Araliaceae/Apiaceae, thus, is not surprising. In addition, polyacetylenes are characteristic of the Asterales/Campanulales (Dahlgren, 1983; see also Wagenitz, 1992). Cladistic analyses of *rbc*L sequence data strengthens the hypothesis that Araliales, Dipsacales, and Asterales are related (Donoghue et al., 1992; Olmstead et al., 1992; Plunkett et al., 1992).

Characters 2, 14, and 17, are multistate, and were considered to be unordered in the computer analyses. Palmately and pinnately compound leaves, as well as deeply dissected leaves, have not been distinguished in this preliminary analysis; all are considered derived in relation to simple leaves. Eyde and Tseng (1971), however, considered palmate leaves to be derived in comparison with pinnate leaves, and suggested that this feature could be useful in dividing the Araliaceae into two major subgroups (Eyde & Tseng, 1971, fig. 9). Unifoliate leaves are also common in Araliaceae, and likely have originated several times.

In the Araliales, perforation plate form varies more or less continuously from simple to scalariform (Rodríguez, 1957, fig. 66, and 1971, fig. 5). It is correlated with vessel element length and end-wall angle, which also vary essentially continuously (Rodríguez, 1957, figs. 64 and 65). Because assignment of character state was difficult and somewhat arbitrary, perforation plate form was not included in our analyses.

Results. The PAUP analysis resulted in the generation of a single most parsimonious tree (Fig. 2) of 25 steps and CI of 0.84 (or 0.80 excluding characters uninformative within the in-group); the RI is 0.88. This cladogram indicates that Araliaceae, as currently delimited (Takhtajan, 1980; Dahlgren, 1980; Cronquist, 1981), are paraphyletic. Apiaceae are polyphyletic, being derived twice within Araliaceae.

The araliaceous genus *Myodocarpus*, a New Caledonian endemic, is united with the clade that includes Apioideae and Saniculoideae (of Apiaceae). They have in common laterally flattened fruits, a well developed carpophore (char. 15; see Baumann, 1946, figs. 9, 20-23), vittae-like schizogenous cavities (char 14; or Sekretbehälter, see Baumann, 1946, figs. 17, 18), and reduced endocarp (char. 17-2; Baumann, 1946, figs. 18, 19). It is noteworthy that some drupaceous members of the Araliaceae possess a carpophore, e.g., *Stilbocarpa*, while others often have 2-carpellate, laterally compressed fruits, e.g., *Merrilliopanax*, some species of *Acanthopanax* and *Anomopanax* (Li,

TABLE 6. Araliaceae/ApiaceaeMatrix (*= characters with notes; a = {0/1}

	** *	*	**	
		1		
	12345	67890	12345	678
Pittosporum	00000	0000a	00000	000
Aralia	01111	01010	10000	010
Schefflera	01111	01110	10000	010
Dendropanax	02111	01110	10000	010
Oreopanax	01111	01110	10000	010
Myodocarpus	01111	01111	10111	020
Apium	11101	11111	10121	120
Chaerophyllum	11101	11111	10121	120
Eryngium	11101	01111	11121	021
Sanicula	11101	01111	11120	021
Hydrocotyle	10111	01111	10100	010
Centella	10111	01111	10100	010

1: A few (presumably derived) species of *Aralia* are herbaceous (Graham, 1966); a few species of *Eryngium* are woody (Rodríguez, 1957). **2:** In *Aralia* and *Myodocarpus* leaves are once to several times pinnately compound (considered ancestral by Eyde and Tseng [1971], who derived Araliales from Rutales); palmately compound (or unifoliate) in *Schefflera* and *Oreopanax*; dissected in *Apium, Chaerophyllum, Eryngium,* and *Sanicula*. **4:** Although stipules are lacking from adult leaves of *Apium, Chaerophyllum, Eryngium,* and *Sanicula*, stipule-like flanges may be present on rosette leaves of some Apiaceae, e.g., *Apium, Chaerophyllum, Foeniculum,* and *Heracleum*; *Cicuta* even has such structures on adult leaves (W. Judd, pers. observations). **10:** A few (presumably derived) species of *Aralia* and *Schefflera* have only two carpels (Li, 1942; Eyde and Tseng, 1971). **14:** Globular schizogenous oil cavities or proto-vittae (Sekrebehälter of Baumann, 1946) are present in *Myodocarpus*; these are considered ancestral to elongate oil cavities/canals or vittae (Baumann, 1946). These should not be confused with resin canals, which occur in the fruits of Araliaceae and Apiaceae (all subfamilies), and may be associated with the vascular bundles (Baumann, 1946) or scattered in the mesocarp (Eyde and Tseng, 1971); in *Hydrocotyle* and *Centella* vittae are lacking, but scattered oil cells ("Sekretzellen") are present (Baumann, 1946). **15:** Carpophore reduced in *Eryngium* and absent in *Sanicula*, presumably by reduction (Baumann, 1946; Jackson, 1933; Rogers, 1950).

1942; Baumann-Bodenheim, 1955; Eyde & Tseng, 1971). Species with 2-carpellate gynoecia appear to have evolved several times within Araliaceae (Table 6, and Eyde & Tseng, 1971). The oil cavities are globular in *Myodocarpus*, but are elongated in the more specialized fruits of Apioideae and Saniculoideae. *Myodocarpus* has retained plesiomorphic araliad vegetative features, such as a woody habit, pinnately compound leaves, stipules, and a panicle-like cluster of umbels (Baumann, 1946, fig. 8).

The vessel-elements of *Myodocarpus*, elongate with scalarform perforation plates (Rodríguez, 1957, figs. 6g, 64, and 66), are plausibly also a retained plesiomorphic feature. For the reasons given above this feature was not included in our analyses. *Pittosporum* (our outgroup) possesses vessel elements with simple perforations (except in a single New Caledonian endemic in which they are scalariform; see Carlquist, 1981), as do all genera of Apiaceae included in our analysis. In contrast, some genera of Araliaceae, e.g., *Myodocarpus, Astrotrichia, Schefflera, Plerandra,* have vessel elements with scalariform perforations that have few to fairly numerous (up to ca. 25) cross-bars (Rodríguez, 1957, 1971; Cronquist, 1981). The vessel elements in these araliaceous genera could be interpreted as a retained ancestral condition (see Bailey, 1944; Dickison, 1975); thus it is likely that vessel elements with simple perforations evolved independently in Pittosporaceae, Apiaceae, and some Araliaceae, e.g., *Oreopanax*. It is noteworthy that vessel elements with scalariform perforation plates are present in more distant outgroups, i.e., Cornaceae, the "woody

Saxifragaceae," some Rutaceae, and (see below) Dipsacales (Rodríguez, 1971; Eyde & Tseng, 1971). Preliminary analyses including perforation plate form resulted in a tree basically similar to that presented in Figure 2. The only topological effect resulting from the inclusion of this feature is the introduction of a node separating *Oreopanax* from *Dendropanax* and *Schefflera*, with *Oreopanax* linking with Apiaceae and *Myodocarpus*.

Representatives of Apioideae and Saniculoideae form the monophyletic sister-group of *Myodocarpus* and share the synapomorphic loss of stipules (char. 4), the presence of elongated schizogenous oil cavities (or vittae; char. 14-2), and probably the herbaceous habit (char. 1). This clade contains some woody taxa, e.g., some species of *Eryngium* (Saniculoideae), *Heteromorpha, Bupleurum*, and *Myrrhidendron* (Apioideae; Rodríguez, 1957). However, the wood of these genera is much more advanced than that of *Myodocarpus* (Rodríguez, 1957). The herbaceous habit evolved either once in Apioideae/Saniculoideae (with several reversals; see Fig. 2) or several times (with certain genera retaining the woody condition). In any case, the feature likely is homoplastic, with woody species occurring in several tribes (Rodríguez, 1957). Both the Apioideae and Saniculoideae are probably monophyletic (see apomorphies in Fig. 2).

The *Myodocarpus*-Apioideae-Saniculoideae clade probably is the sister group to Hydrocotyloideae, as represented by *Hydrocotyle* and *Centella*. This grouping is supported by the shared possession of 2-carpellate, schizocarpic fruits (chars. 10, 13). Most genera of Araliaceae have retained the ancestral drupaceous fruit, and all schizocarpic members of Araliales likely form a monophyletic group. It is noteworthy that Hydrocotyloideae have retained the plesiomorphic features of stipulate leaves and fruits with bony endocarps, but have evolved the herbaceous habit independently of Apioideae-Saniculoideae.

Relationships among the "basal" genera in Figure 2 are poorly resolved. There is no evidence, however, that these genera form a monophyletic group.

The monophyly of the Araliaceae/Apiaceae clade is very clear, if Pittosporaceae are taken as first outgroup and Asterales (incl. Campanulales) as second outgroup. The group (often treated at the ordinal level, see Cronquist, 1968, 1981, 1988) is characterized by the following synapomorphies (some of which show reversals): compound leaves with sheathing petiole bases (chars. 2, 3), stipules (char. 4), umbellate inflorescences (char. 5), minute calyx (char. 7), inferior ovary capped by nectariferous tissue (the stylopodium) (chars. 9, 11), and fleshy fruits with several pits, i.e., endocarp well developed (char. 17). The presence of a corolla of separate petals (a likely reversal, see above) is probably synapomorphic at this level. Chemical features, e.g., storage of carbohydrates as the trisaccharide umbelliferose, endosperm with petroselinic acid (Hegnauer, 1971; Cronquist, 1981), also unite this complex.

Discussion. The results of this preliminary cladistic investigation support the view of Thorne (1973a), who, on phenetic criteria, merged Araliaceae and Apiaceae into a single family, i.e., Araliaceae s.l. He stated: "My acceptance of the Apiaceae as a distinct family was not really seriously shaken until I spent a year and a half (1959-1960) in Australasia, where I came in close contact with the Hydrocotyloideae, Mackinlayeae, and Myodocarpeae, especially the New Caledonian *Myodocarpus*. It is much harder to ignore intermediate taxa when one has studied and collected them where they are indigenous" (Thorne, 1973a, p. 162), and added that "I do not consider the gaps among the four taxa [Araliaceae, Apioideae, Saniculoideae, Hydrocotyloideae] of more than subfamilial significance," (Thorne, 1973a, p. 163; 1983). Thorne (1973a) also considered the Apiaceae, as traditionally circumscribed, to be polyphyletic. He considered the possibility of recognizing four families, i.e., Araliaceae, Apiaceae, Saniculaceae, and Hydrocotylaceae, but concluded by suggesting that "phylogeny and the teaching of taxonomy seem much better served by retaining the four groups . . in the Araliaceae" (Thorne, 1973a, p. 163). Recently, however, he has altered this view, accepting three families: Araliaceae, Hydrocotylaceae, and Apiaceae (Thorne, 1992a, 1992b), because his merging of Araliaceae and Apiaceae had received very little support from the botanical community

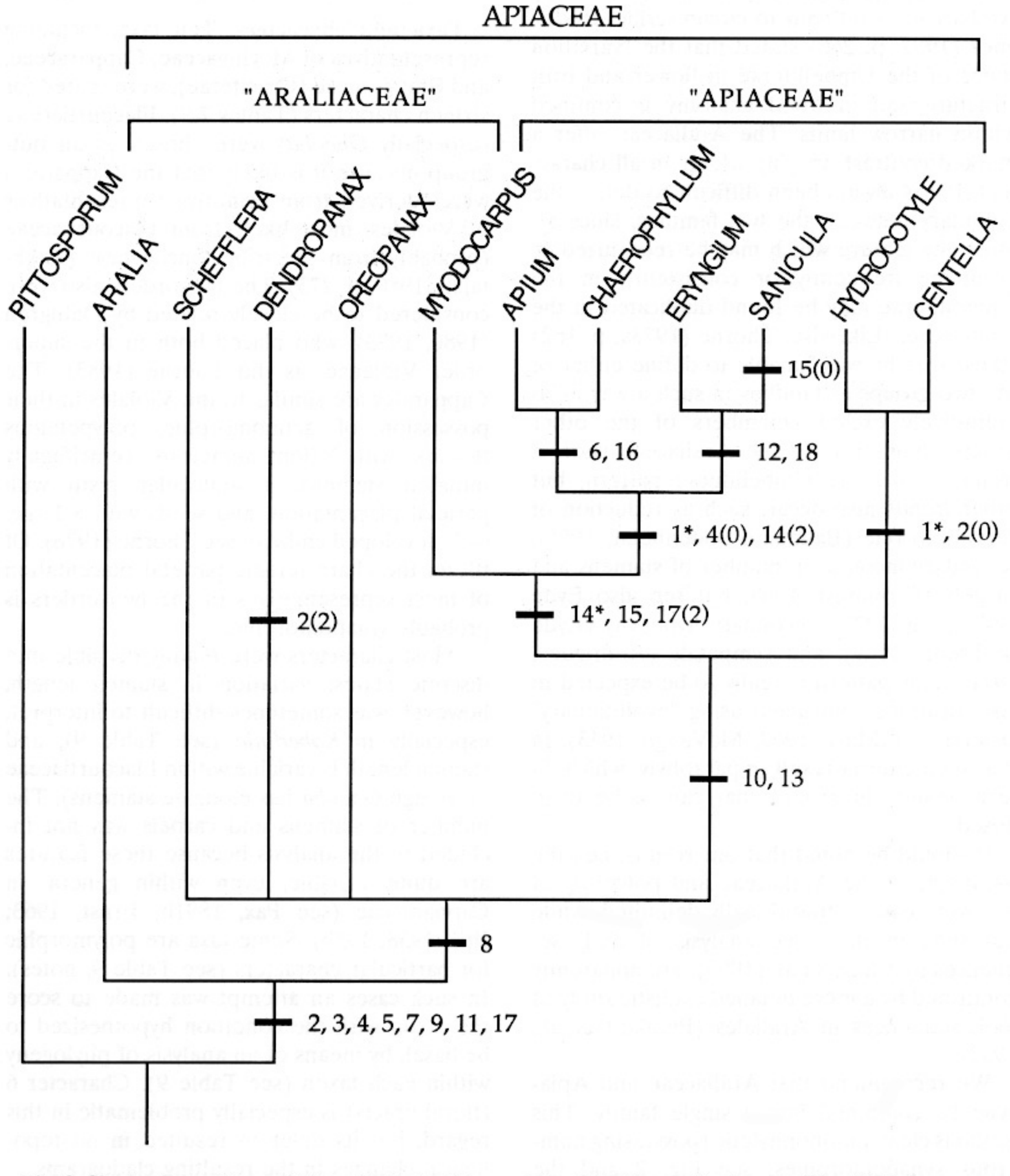

Fig. 2. Single shortest tree (25 steps) obtained in analysis of Araliaceae/Apiaceae; CI = 0.84. * = one or more alternative placements are equally parsimonious; char. 14 equivocal only when considered unordered.

(Thorne, pers. comm.). We note that the recognition of several families does not alter the paraphyly of the Araliaceae.

Constance (1971) provided a detailed taxonomic history of the Apiaceae. This family was first included in Araliaceae by Adanson (1763). These families also were merged by Baillon (1867-1895) and Hallier (1905). Our cladogram also lends support to Rodríguez (1957, p. 263), who stated that on anatomical grounds "it is difficult to derive either the Apioid or the Saniculoid types from the Hydrocotyloideae as they now exist," and to Baumann (1946, p. 109), who wrote that "the Umbelliferae are a specialized tribe of the Araliaceae."

As is typical of paraphyletic taxa, the family Araliaceae, is difficult to circumscribe. Rodríguez (1957, p. 266) stated that the "variation range of the Umbelliferae in flower and fruit structure and in wood anatomy is confined within narrow limits. The Araliaceae offer a marked contrast, varying widely in all characters. It has always been difficult to define the boundary between the two families, since almost any feature which may be recognized as occurring frequently or consistently in the Umbelliferae may be found duplicated in the Araliaceae." Likewise, Thorne (1973a, p. 162) stated that he was "unable to define either of the two groups as families in such a way as to definitively exclude members of the other group." Not only do the Araliaceae show a trend toward the Umbelliferae pattern, but other trends also occur, such as reduction of carpels to one (Baumann-Bodenheim, 1955), secondary increase in number of stamens and carpels (Cronquist, 1968; but see also Eyde and Tseng, 1971), secondary hypogyny (Eyde & Tseng, 1969), and sympetaly (Rodríguez, 1971). This pattern is really to be expected in classifications contructed using "evolutionary" criteria (see Mayr, 1969; McVaugh, 1943), in that such criteria result in paraphyly, which, in turn, results in groups that cannot be diagnosed.

It should be noted that our results, i.e., the paraphyly of the Araliaceae and polyphyly of the Apiaceae, as traditionally delimited, while not seen in the large analysis of *rbc*L sequences by Chase et al. (1993), are apparently confirmed by a more detailed cladistic study of *rbc*L sequences in Araliales (Plunkett et al., 1992).

We recommend that Araliaceae and Apiaceae be combined into a single family. This group is clearly monophyletic (possessing numerous synapomorphies, see Fig. 2 and the enumeration above). The combined family must be called Apiaceae or Umbelliferae, even though Araliaceae has priority; see Table 19, and the International Code of Botanical Nomenclature, Appendix IIB (Greuter, 1988). Thus, the name Apiaceae is redefined to refer to the most recent common ancestor of plants previously considered to be Apiaceae (all three subfamilies, see Table 4) and Araliaceae, and all of the descendents of that ancestor.

CAPPARACEAE AND BRASSICACEAE

Taxa and characters. Ten taxa, including representatives of Moringaceae, Capparaceae, and Brassicaceae (Cruciferae), were scored for sixteen characters (Tables 7-9). Flacourtiaceae (especially *Oncoba*) were chosen as an outgroup because it is likely that the Capparales were "derived from primitive representatives of Violales, most likely from Flacourtiaceae (probably from the tribe Oncobeae)" (Takhtajan, 1980, p. 273). The two orders also were considered to be closely related by Dahlgren (1980, 1983), who placed both in the superorder Violanae, as did Thorne (1983). The Capparales are similar to the Violales in their possession of actinomorphic, polypetalous flowers with often numerous centrifugally initiated stamens, a unilocular pistil with parietal placentation, and seeds with a large, well-developed embryo; see Thorne (1976). Of these, the characteristic parietal placentation of most representatives of the two orders is probably synapomorphic.

Most characters were readily divisible into discrete states; variation in stamen length, however, was sometimes difficult to interpret, especially in *Koberlinia* (see Table 9), and stamen length is variable within Flacourtiaceae (although *Oncoba* has elongate stamens). The number of stamens and carpels was not included in the analysis because these features are quite variable, even within genera, in Capparaceae (see Pax, 1891b; Ernst, 1963; Iltis, 1958, 1959). Some taxa are polymorphic for particular characters (see Table 9, notes). In such cases an attempt was made to score the taxon with the condition hypothesized to be basal, by means of an analysis of phylogeny within each taxon (see Table 9). Character 6 (floral bracts) is especially problematic in this regard, but its deletion resulted in no topological changes in the resulting cladograms.

Results. The initial PAUP analysis resulted in the discovery of four equally parsimonious trees of 30 steps and a CI of 0.60 (or 0.57 when characters uniform within the ingroup are disregarded) and a RI of 0.60. These differ in the relative position of *Moringa*, *Tovaria*, *Koeberlinia* and *Crateva*. In three of the trees *Moringa* is a basal branch, with all other taxa linked by 4-merous flowers (char. 8) and seeds with a curved embryo (char. 15).

TABLE 7. Capparaceae/Brassicaceae Taxa[*]

- **Capparaceae** s. l.
    - Tovarioideae
        - *Tovaria*
    - Koeberlinioideae
        - *Koeberlinia*
    - Capparoideae
        - *Capparis*
        - *Crateva*
    - Cleomoideae
        - *Cleome*
        - *Polanisia*
- **Brassicaceae**
    - *Descurainia*
    - *Warea*
- **Moringaceae**
    - *Moringa*
- **Flacourtiaceae**
    - *Oncoba* (OG)

[*] Classification based on Thorne (1992b)

In the fourth tree, however, *Moringa* and *Tovaria* form a clade on the basis of compound leaves and flowers with short stamens (chars. 4 and 11), with the 4-merous flowers and curved embryo of *Tovaria* considered to have evolved in parallel in other Capparales. This topology, which joins *Tovaria* and *Moringa* on the basis of otherwise homoplasious and fairly simple characters, while postulating independent origins of curved embryos and 4-merous flowers is considered implausible. Analyses weighting either character 8 or 15 by a factor of two resulted in the discovery of only three most parsimonious trees, i.e., those with *Moringa* positioned as the sister group of the remaining glucosinolate taxa. We also note that cladistic studies based on *rbc*L sequence data are consistent with this arrangement (Chase et al., 1993; Rodman et al., 1993). Only the trees with *Moringa* basal are considered further, and only these trees are used as the basis for our taxonomic conclusions. A representative cladogram and the strict consensus of the three *Moringa*-basal trees are presented in Figures 3 and 4.

These cladograms indicate that Capparaceae, as variously delimited in current evolutionary classifications (Takhtajan, 1980; Dahlgren, 1980; Cronquist, 1981; Thorne, 1983), are paraphyletic. *Cleome* and *Polanisia* (representatives of Capparaceae subfam. Cleomoideae) are hypothesized to share a more recent common ancestor with *Warea* and *Descurainia* (representatives of Brassicaceae) than with other genera of Capparaceae, i.e., *Capparis* and *Crateva* (of subfam. Capparoideae), *Koeberlinia* (subfam. Capparoideae of Thorne, 1983, 1992a; but variously placed, see Rodman, 1991a & b; Thorne 1992b), and *Tovaria* (subfam. Tovarioideae of Thorne, 1983, 1992a, 1992b; but see also Cronquist, 1981). The Cleomoideae and Brassicaceae share the following synapomorphies: the presence of a thickened replum (specialized placenta--char. 12; see Iltis, 1957; Al-Shehbaz, 1984) in the fruit, dehiscent (and silique-like) fruit, in which the valves break away from the persistent replum, and herbaceous habit (char. 1).

Brassicaceae are considered to be monophyletic because they share these distinctive apomorphies: an ovary with a false septum (char. 13), which persists in the mature fruit (i.e., the fruits are siliques), and seeds in which the embryo is strongly folded (not just curved; char. 15-2). The last feature is correlated with the loss of the seed-invagination characteristic of Capparaceae (Pax, 1891b). Here it is of interest that the seed-invagination of Cleomoideae is present but narrower than that of Capparoideae. The seeds of Brassicaceae also are distinctive because of their three-layered testa, a possible synapomorphy (Vaughan & Whitehouse, 1971).

Warea retains. several plesiomorphic features such as the presence of an elongate gynophore (reduced in *W. carteri*), long exserted (and only very slightly to not at all tetradynamous) stamens, and glandular stipules (in the inflorescence). In addition, it is most parsimonious to interpret the elongate fruits of *Warea* and *Descurania* as retained ancestral features, with short fruits (as present in many Brassicaceae; see Al-Shehbaz, 1984) interpreted as derived from the elongate condition.

Obviously, some members of the Brassicaceae have indehiscent (or unusually dehiscent) fruits in which the false septum is modified (or even lacking). These, however, appear to be secondarily derived from silique-like fruits (with a false septum), the ancestral condition within Brassicaceae. We presume that such apomorphies within Brassicaceae do

TABLE 8. Capparaceae/Brassicaceae Characters

1. Habit: woody (0), herbaceous (1)
2. Myrosin Cells and Glucosinolates: absent (0), present (1)
3. Multicellular Gland-headed Hairs: absent (0), present (1)
4. Leaves: simple (0), pinnately/palmately compound (1)
5. Stipules: present (0), absent (1)
6. Flower Bracts: present (0), absent (1)
7. Flower Symmetry: actinomorphic (0), zygomorphic (1)
8. Flower Merosity: 5-merous (0), 4-merous, petals 8 (1), 4-merous, petals 4 (2)
9. Perianth Aestivation: closed (0), open (1)
10. Gynophore (or androgynophore): more or less absent (0), elongate (1)
11. Stamen Length: elongate, exerted (0), shorter than or equalling perianth (1)
12. Replum/Fruit Dehiscence: absent, fruits indehiscent (or not as follows) (0), present, fruits dehiscent (silique-like, valves falling away from persistent replum) (1)
13. Ovary Locules: unilocular, false septum lacking (0), bilocular, with false septum (1)
14. Ovary/Fruit Shape: short, globose or ovoid (0), elongate (1)
15. Embryo: straight (0), curved, seed with invagination (wide to narrow) (1), folded, seed lacking invagination (2)
16. Endosperm: more or less copious (0), scanty or absent (1)

not affect the phylogenetic placement of the family relative to other taxa.

Although relationships among genera of Capparaceae are incompletely represented in this analysis, *Capparis* may be related to Brassicaceae and Cleomoideae on the basis of its elongate fruit (char. 14). Among sampled genera of Capparaceae, *Tovaria* and *Koeberlinia* are seen to be more distantly related (Fig. 3), in part because they lack a conspicuous gynophore. *Tovaria* also is distinctive due to its flowers with eight petals and sepals, and axile placentation (which here is interpreted as derived from the parietal condition; see Pax, 1891a; Cronquist, 1981). *Koeberlinia* is marked by very reduced leaves and thorny branches, and a lack of glucosinolates (Rodman, 1981, 1991a & b), although myrosin cells are present. The studies of Rodman (1991b) and Rodman et al. (1993) suggested that these genera should be placed in separate families, i.e., Tovariaceae and Koeberliniaceae.

In an effort to clarify the phylogenetic position of *Koeberlinia* and *Tovaria* (as well as *Crateva*; see Figs. 3 & 4) we conducted a supplemental analysis that included *Reseda* (representing Resedaceae; Table 9), as suggested by *rbc*L sequence-based analyses (Rodman et al., 1993). This analysis resulted in the discovery of a single most parsimonious tree of 31 steps (and CI of 0.58); this tree is identical to that of Figure 3, except that *Reseda* is included and positioned along the internode between *Koeberlinia* and *Tovaria*. In this tree *Crateva* forms a monophyletic group along with *Capparis*, *Cleome*, *Polanisia*, *Warea*, and *Descurainia* on the basis of an elongate gynophore. *Reseda* (Resedaceae) is hypothesized as monophyletic on the basis of its zygomorphic corolla (of fringed-appendiculate petals) and, of course, its distinctive syncarpous gynoecium that is open at the apex and bears several, small, sessile stigmas around the rim. Clearly, this supplemental analysis supports the cladogram topology presented in Figure 3, and indicates that *Tovaria* and *Koeberlinia* are probably best excluded from Capparaceae.

The Capparales are considered to be monophyletic, as indicated by seeds with endosperm scanty to lacking (char. 16) and the presence of myrosin (in spherical idioblasts) and glucosinolates (char. 2; mustard-oil glucosides; see Ettlinger & Kjaer, 1968; probably lost in *Koeberlinia*, see Table 9, footnotes; Rodman 1991a & b). The presence of glucosinolates is correlated with the possession of endoplasmic reticulum with dilated cisternae (see Iversen, 1970; Behnke, 1977; Jorgensen, 1981), likely an additional synapomorphy. In some trees compound leaves (char. 4) are hypothesized as a basal synapomorphy of Capparales, while in others (Fig. 3) this feature evolved three times (i.e., in *Tovaria*, *Crateva*, and Cleomoideae); in either case it is homoplasious.

TABLE 9. Capparaceae/Brassicaceae Matrix (*=characters with notes; a ={0/1})

										*						
	*	*	*	*	*	*	*	*	*	1				*		*
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Oncoba	0	0	0	0	0	0	0	0	0	0	a	0	0	0	0	0
Moringa	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	1
Tovaria	1	1	0	1	1	0	0	1	0	0	1	0	0	0	1	1
Crateva	0	1	0	1	0	0	0	2	1	1	0	0	0	0	1	1
Capparis	0	1	0	0	0	0	0	2	0	1	0	0	0	1	1	1
Koeberlinia	0	1	0	0	1	0	0	2	0	0	0	0	0	0	1	1
Cleome	1	1	1	1	0	0	1	2	0	1	0	1	0	1	1	1
Polanisia	1	1	1	1	0	0	1	2	1	0	0	1	0	1	1	1
Warea	1	1	0	0	0	1	0	2	0	1	0	1	1	1	2	1
Descurainia	1	1	0	0	1	1	0	2	0	0	1	1	1	1	2	1
supplemental taxon - (see discussion in text)																
Reseda	a	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1

1: Character state delimitation sometimes ± equivocal; *Tovaria* is scored as herbaceous, although it can be suffrutescent; Cronquist (1981, p. 442) noted that these plants are "coarse herbs, soft-shrubs, or half-shrubs." **2:** *Koeberlinia* contains myrosin cells (Gibson, 1979) although it appears to lack glucosinolates (Rodman, 1981, 1991a). Myrosin cells contain myrosinase, the hydrolytic enzyme that catalyzes the breakdown of glucosinolates, and as Rodman (1991a, p. 600) noted, "the paradoxical situation exists [in *Koeberlinia*] of a plant producing an utterly functionless enzyme." *Koeberlinia* is considered to have lost glucosinolates, perhaps with the acquisition of its distinctive xeromorphic habit. Presence of glucosinolates in *Moringa*, Capparaceae, and Brassicaceae taken from the literature, see Cronquist (1981), Rodman (1981, 1991a). **3:** Multicellular glandular hairs lacking in *Descurainia*, but such hairs are present in a few species of Brassicaceae (Al-Shehbaz, 1984); a few species of *Cleome* lack glandular hairs, a condition considered to be an evolutionary loss. **4:** Leaves 2 or 3 times pinnately compound in *Moringa*; palmate to trifoliate in other taxa with compound leaves. The leaves of *Koeberlinia* are reduced and scale-like. Some derived species of *Cleome* have reduced, unifoliate leaves (Iltis, 1959; Ernst, 1963). Some members of Brassicaceae have deeply dissected leaves, but these are not truly compound, and are certainly not homologous with the compound leaves of *Cleome*, *Tovaria*, etc. **5:** Stipules are sometimes lacking in *Moringa*. They may be present (and minute) or lacking in *Cleome* (Iltis, 1958, 1959); presence is considered ancestral. Stipules are hypothesized to be present in *Warea* only in the form of small glands paired at the base of the floral pedicels. If the scoring of *Warea* is changed to 1 for this feature, the resulting cladograms remain unchanged. **6:** Inflorescence bracts are rarely lacking in *Cleome*, and are present in some Brassicaceae. **7:** *Warea* and *Descurainia* have actinomorphic flowers, and this character is considered to be ancestral in the Brassicaceae; some genera, e.g., *Teesdalia*, *Iberis*, however, have evolved zygomorphic flowers. **8:** Although the number of sepals and petals of Residaceae is often 6, this group is considered to have basically 4-merous flowers (i.e., state 1) because the number of sepals and petals varies from 4 to 8. **9:** Some species of *Cleome* have open aestivation like that of *Polanisia* (see Iltis, 1958); it is likely that this is a synapomorphic similarity and that *Cleome* is paraphyletic (also see Iltis, 1957; Bremer and Wanntorp, 1978). **10:** Some species of *Cleome* have a short gynophore; this is interpreted as a reduction of the elongate gynophore characteristic of some species (Iltis, 1958, fig. 3). A very short gynophore is present in *Reseda*; this is interpreted as a character state distinct from the elongate gynophore of *Crateva*, *Capparis*, etc. **14:** A few species of *Capparis* and of *Cleome* have short ovaries. **16:** *Tovaria* has better developed endosperm than other Capparales; however, it is still described as "rather thin" (see Cronquist, 1981).

Among sampled taxa, *Moringa* is the sister taxon to the remaining glucosinolate taxa. All other in-group taxa possess the additional derived characters of a curved embryo (char. 15) and 4-merous flowers (char. 8), while *Moringa* has retained the straight embryo and 5-merous flowers characteristic of the Violales. It is also clear from the cladogram (Fig. 3) that the zygomorphy of the 5-merous flowers of *Moringa* is quite distinct from that of the 4-merous

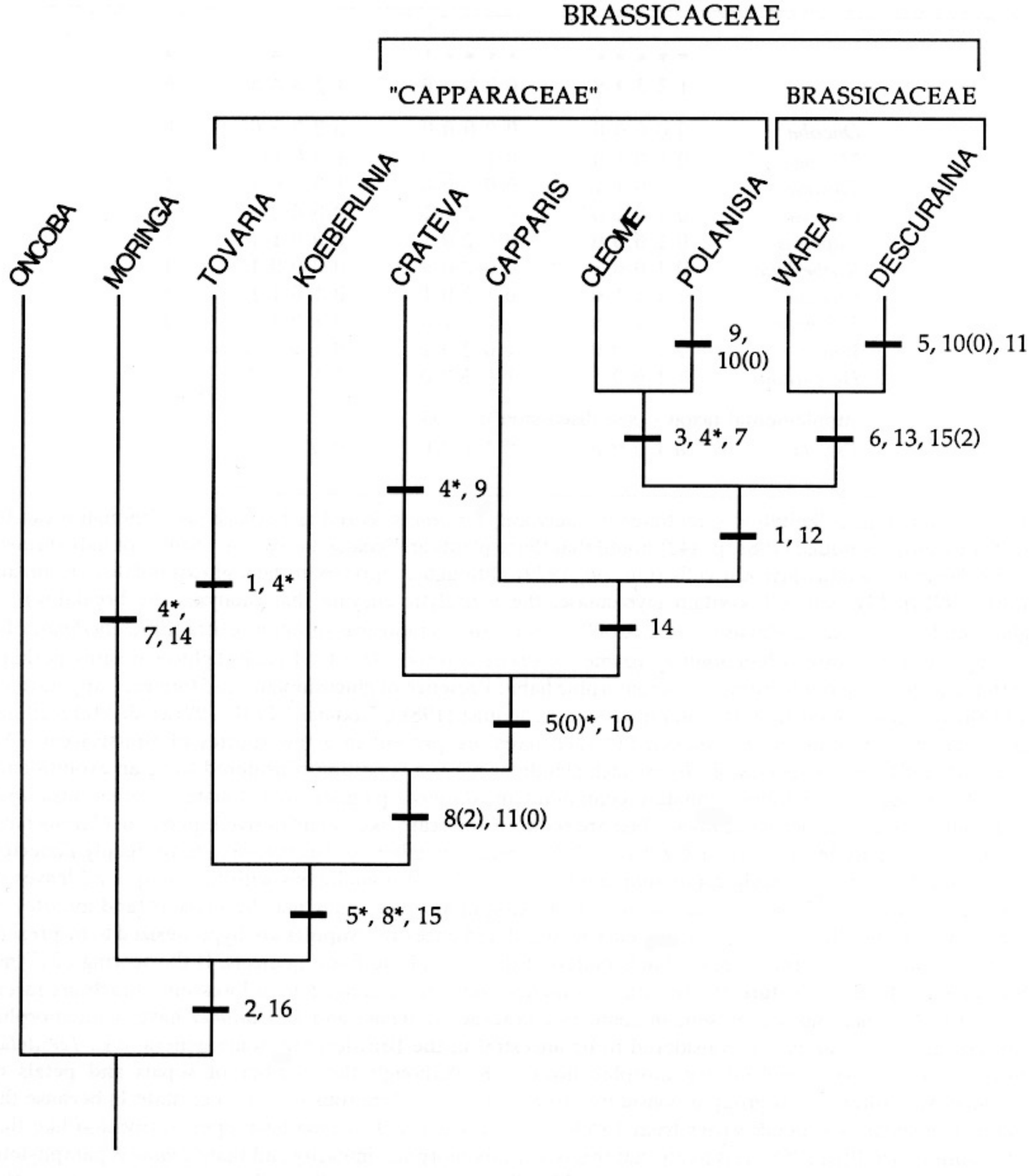

Fig. 3. Representative tree (30 steps; with *Moringa* as sister group to remaining taxa) resulting from analysis of Capparaceae/Brassicaceae; CI = 0.60. * = one or more alternative placements are equally parsimonious.

flowers of *Cleome* and *Polanisia*, and some Brassicaceae, and has evolved independently (Fig. 3). *Moringa* is also very distinctive owing to its petaloid calyx, hypanthium, unusual androecium of 5 curved stamens alternating with staminodia, usually 3-angled, elongate fruit, 2 or 3-times pinnately compound leaves, and seeds with a thickened mesotestal layer (Corner, 1976).

Discussion. The results of this preliminary cladistic investigation not only strongly support the widely held view that Capparaceae and Brassicaceae are nearest relatives (Rollins, 1956; Iltis, 1957; Ernst, 1963; Al-Shehbaz, 1973, 1984), but also the hypothesis that Capparaceae subfam. Cleomoideae is the sister group of Brassicaceae; see Payson (1923), Janchen (1942), Dvorak (1973), and Hauser & Crovello (1982). Takhtajan (1980, p. 273), for example, stated that the Brassicaceae were "derived from Capparaceae-Cleomoideae and linked to them through the tribe Stanleyeae [=Thelypodieae]." Al-Shehbaz (1973, pp. 76, 77) noted that some "of the features considered to be primitive in these genera [i.e., *Stanleya* and *Warea*, of the Thelypodieae] are: long and exserted filaments that are equal in length; long and curled anthers; densely-flowered inflorescences; sessile stigmas; and usually long gynophores." He added that, "These are some of the important features that are shared by the two genera and some members of the subfamily Cleomoideae-Capparaceae."

A sister-group relationship of Cleomoideae and Brassicaceae, however, often has been disputed. Al-Shehbaz (1984, p. 346) stated that "although the morphological evidence very strongly favors a connection [of Capparaceae-Cleomoideae and Brassicaceae] through the Thelypodieae, none of the extant crucifers is truly archaic, and the palynological data . . . do not support such a direct link. It is therefore more reasonable to assume that the connection between the two families is through a common ancestor." Cronquist (1981) expressed a similar view. Although he stated (p. 445) that "the Cleomoideae approach the Brassicaceae" and (p. 449) that the "cruciferous gynoecium is surely homologous with the gynoecium of those Capparaceae that have a replum but lack a partition," he concluded (p. 449) that he was "inclined toward" the view that "the similarities between *Stanleya* (a selenophile) and genera such as *Cleome* reflect parallelism or convergence rather than close relationship."

As noted above, palynological variation within Capparales influenced thinking on relationships within the order. The pollen of Capparaceae is smooth to shallowly reticulate (or spinose) with neither columellae nor lumina recognizable, while in pollen of Brassicaceae the reticulum is very strongly defined and clearly elevated by columellae (Al-Shehbaz, 1973). In addition, the pollen of Brassicaceae are colpate while those of Cleomoideae are colporate. Erdtman (1971) considered the pollen of these two families to be similar; however, Al-Shehbaz (1973, p. 54) stated that "the similarities between them appear to be less significant than previously supposed" and noted that "grains of the Thelypodieae are typically cruciferous and pollen data alone do not seem to support the suggestion that the tribe is intermediate between the rest of the Cruciferae and the Cleomoideae."

Thelypodieae are clearly linked with other crucifers, as all members of the Brassicaceae are united by several synapomorphies (Fig. 3). Likewise, the view that Capparaceae and Brassicaceae share a common ancestor is supported (Figs. 3 & 4). However, an argument based on the phenetic gap in pollen morphology between the Thelypodieae and Cleomoideae does not deny the possibility of a sister group relationship between the Cleomoideae and Brassicaceae. The distinct reticulum seen in Thelypodieae is simply a synapomorphy of Brassicaceae. It is possible that Brassicaceae, with their strongly reticulate grains, evolved from ancestors with only slightly reticulate grains (as in Cleomoideae).

Our results support the view that there are just as many carpels in the gynoecium of crucifers as indicated by the number of placentae (see Puri, 1950, 1951), in contrast to the tetracarpellary theory of Eames and Wilson (1928). The 2-carpellate condition of Cleomoideae and Brassicaceae has been inherited from the gynoecial condition of their common ancestor.

In summary, Capparaceae, as currently delimited, are paraphyletic, and Cleomoideae are more closely related to Brassicaceae than to Capparoideae (Figs. 3 & 4). It is noteworthy that the paraphyly of the Capparaceae, as well as the "more basal" position of *Tovaria*, *Koeberlinia*, and especially *Moringa*, also has been documented in a recent cladistic study (Rodman et al., 1992, 1993) based on cpDNA *rbc*L sequence data.

In this analysis *Cleome* is more closely related to a clade containing *Brassica* than it is to *Capparis*; *Reseda* is positioned as the sister taxon to the *Capparis-Cleome-Brassica* clade; *Tovaria* and *Koeberlinia* are "more basal", with *Moringa* positioned near the "base" of the glucosinolate clade.

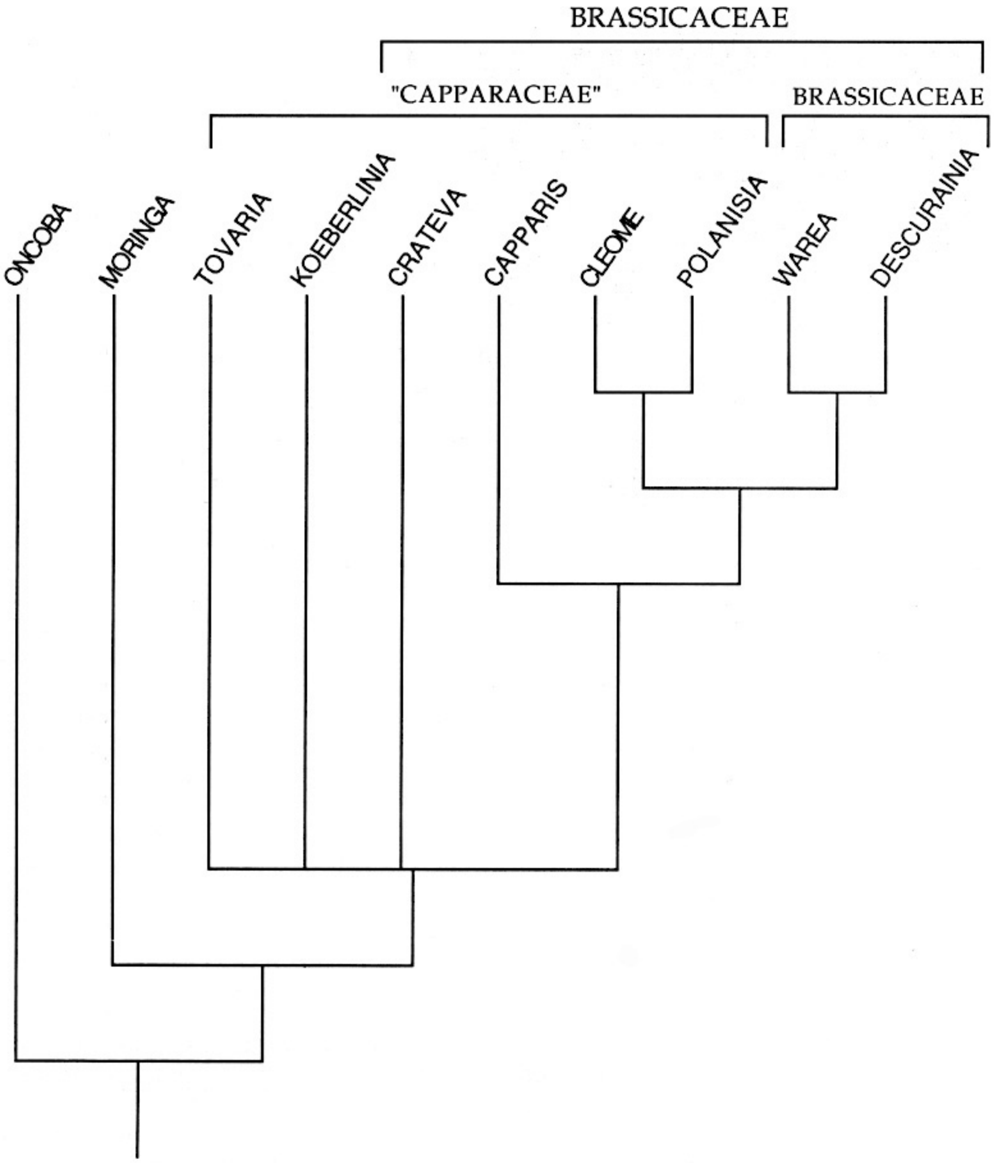

Fig. 4. Strict consensus of 3 trees (with *Moringa* as sister group to remaining taxa) resulting from analysis of Capparaceae/Brassicaceae.

We suggest the following taxonomic solution which is based upon our own analysis and on studies of *rbc*L sequences. Brassicaceae and Capparaceae s.s. should be united in a single family. The name of this family must be Brassicaceae (Cruciferae) despite the fact that Capparaceae has priority (see Table 19).

The name Brassicaceae is redefined to refer to the most recent common ancestor of plants previously considered to be Brassicaceae as well as to those plants assigned to Capparaceae (but excluding *Tovaria* and *Koeberlinia*; Table 7), and to all of the descendents of that ancestor. Brassicaceae s.s. are monophyletic and should also be recognized. Our cladograms (Fig. 3) also support the "basal" position of *Crateva* within the paraphyletic Capparoideae (see Puri, 1950; DeWolf, 1962).

CAPRIFOLIACEAE, DIPSACACEAE, AND VALERIANACEAE

Caprifoliaceae are generally placed in the Dipsacales, along with Valerianaceae, Dipsacaceae, and Adoxaceae (Donoghue, 1983). Calyceraceae are sometimes included, but morphological and molecular evidence indicates a closer relationship to Asterales (Donoghue, 1983; Olmstead et al., 1992, 1993).

Caprifoliaceae (except *Triosteum* and some *Sambucus*) are woody plants, whereas the other families of Dipsacales consist mainly of herbaceous species. In contrast to our other examples, however, none of the lines of Dipsacales currently inhabit primarily tropical environments. Although there are subtropical elements in Caprifoliaceae, most are found in the North temperate zone; several genera have radiated in the Southern hemisphere, mainly at higher elevations.

Taxa and characters. Seventeen taxa were initially included in our analyses (Table 10). This reduced to fifteen, however, as two pairs of taxa were found to have identical scores in our preliminary matrix (*Weigelia* and *Diervilla*; *Kolkwitzia* and *Abelia*) and were subsequently combined (Table 12). Valerianaceae, Dipsacaceae, and Adoxaceae were treated as single terminal taxa, because in each case presumed synapomorphies have been identified. For example, Valerianaceae are characterized by the virtual absence of endosperm in the mature seeds, Dipsacaceae by an "epicalyx" subtending the flower, and Adoxaceae by "split" stamens. Valerianaceae were scored primarily by reference to *Nardostachys*, which appears to have retained more ancestral states (e.g., unreduced calyx lobes, four stamens) than any other genus (Wilkinson, 1949). *Triplostegia* is not included in our analysis; although it is assigned by some authors to Valerianaceae (e.g., Cronquist, 1981), the presence of an epicalyx suggests a closer relationship to Dipsacaceae (Takhtajan, 1980). The scoring of Dipsacaceae was based on a composite of included genera, as reflected in standard family descriptions (e.g., Cronquist, 1981). *Morina* (frequently segregated as Morinaceae) is not included; it is so highly modified that it is reasonable to assume it would have little influence on basal relationships in Dipsacales (Hofmann and Göttmann, 1990).

TABLE 10. Caprifoliaceae/Dipsacaceae/Valerianaceae Taxa[*]

- **Adoxaceae**
        - *Adoxa*
- **Dipsacaceae**
- **Valerianaceae**
- **Caprifoliaceae** s.l.
    - Sambucoideae
        - *Sambucus*
    - Viburnoideae
        - *Viburnum*
    - Caprifolioideae (Caprifoliaceae s.s.)
        - Caprifolieae
            - *Leycesteria*
            - *Lonicera*
        - Triosteae
            - *Triosteum*
        - Linnaeeae
            - *Abelia*
            - *Dipelta*
            - *Kolkwitzia*
            - *Linnaea*
            - *Symphoricarpos*
        - Diervilleae
            - *Diervilla*
            - *Weigela*
- **Alseuosmiaceae** (OG)
- **Pittosporaceae** (OG)

[*] Classification based on Hara (1983).

Scores for Adoxaceae are based primarily on *Adoxa moschatellina*, as *Adoxa omeiensis* (= *Tetradoxa*) and *Sinadoxa* are still poorly known (Hara, 1983).

Caprifoliaceae are represented in our analysis by twelve of the thirteen commonly recognized genera (Table 10), which allows us to test previous suggestions that the family is paraphyletic (e.g., Donoghue, 1983; see below). In particular, we included representatives of the three subfamilies recognized by Hara (1983; Table 10), and his four tribes of Caprifolioideae (= Caprifoliaceae s.s.; Donoghue, 1983). *Heptacodium* (usually allied with Linnaeeae) is not included because it is still poorly known for some characters, especially ovary anatomy. Several segregate genera have not been treated separately; for example, *Zabelia* (presumably nested within Abelia) and *Macrodiervilla* (of Diervilleae).

Alseuosmia, Periomphale, and *Memecylanthus*, of the Southwest Pacific have sometimes been placed in Caprifoliaceae. However, they

TABLE 11. Caprifoliaceae/Dipsacaceae/Valerianaceae Characters

1. HABIT: woody (0), herbaceous (1)
2. PHYLLOTAXY: alternate (0), opposite (1)
3. LEAF TYPE: simple (0), pinnately compound (1)
4. STOMATA: paracytic (0), anomocytic (1)
5. VESSEL PERFORATIONS: scalariform (0), simple (1)
6. PHELLOGEN: superficial (0), pericyclic (1)
7. INFLORESCENCE: monotelic (0), truncated monotelic (1), polytelic (2) (ordered)
8. SUPERNUMERARY INFLORESCENCE BRACTS: absent (0), present (1)
9. CALYX LOBES: normal (0), very small (1), bristles/pappus (2)
10. CALYX VASCULATURE: 3 traces (0), 1 trace (1)
11. COROLLA TUBE: petals weakly connate at base (0), rotate, small (1), tubular, large (2)
12. COROLLA SYMMETRY: actinomorphic (0), zygomorphic (1)
13. NECTARY TYPE: absent (0), disc (1), multicellular hairs (2), simple hairs (3)
14. NECTARY NUMBER: 5/same as corolla lobes (0), 1/fewer than lobes (1)
15. STAMEN ATTACHMENT: not/slightly adnate (0), adnate to corolla (1)
16. STAMEN NUMBER: 5/same as corolla lobes (or each stamen divided in two) (0), $\leq$ 4/fewer than lobes (1)
17. ANTHER ORIENTATION: introrse (0), extrorse (1)
18. TAPETUM: ameboid (0), glandular (1)
19. POLLEN SIZE/SHAPE: small, prolate (0), large, oblate (1)
20. EXINE STRUCTURE: semitectate, reticulate (0), tectate, columellate (1), tectate, columellae poorly developed (2) (ordered)
21. OVARY POSITION: superior (0), half-inferior (1), inferior (2)
22. OVARY SHAPE: globose, without sterile neck (0), elongate, with neck (1)
23. STYLE/STIGMA: elongate/capitate (0), elongate/lobed (1), short/lobed (2) (ordered)
24. CARPEL NUMBER: 2 (0), 3 (1), 4 or 5 (2)
25. CARPEL ABORTION: all fertile (0), 1 aborts (1), 2 abort (2), 2 abort, ovule displaced (3)
26. CARPEL VASCULATURE: free lateral and dorsal present (0), marginal only (1)
27. OVULE POSITION/VASCULATURE: marginal/single bundle (0), median/double or compound (1)
28. EMBRYO SAC DEVELOPMENT: Polygonum-type (0), Adoxa-type (1)
29. ENDOSPERM DEVELOPMENT: nuclear (0), cellular (1)
30. ENDOSPERM AMOUNT: copious (0), scanty or absent (1)
31. FRUIT TYPE: loculicidal capsule (0), septicidal capsule (1), berry (2), fleshy drupe (3), dry drupe (4), achene (5)
32. MONOTERPENOIDS: absent (0), present (1)
33. FLAVONOIDS: flavonols predominate (0), flavones predominate (1)
34. CHROMOSOME SIZE: large (0), small (1)
35. CHROMOSOME NUMBER: X=9 (0), X=8 (1)

differ in many ways and are most often treated as a separate family, Alseuosmiaceae, believed to be closely related to Escalloniaceae (Airy Shaw, 1932; Donoghue, 1983; Gardner, 1978). More recently, it has been recognized that these genera are related to *Wittsteinia* (formerly of Ericaceae; Dickison, 1986; Donoghue, 1983; Steenis, 1984), and generic limits have been revised accordingly (Steenis, 1984). Alseuosmiaceae are included in our analysis to help root the Dipsacales, based on previous suggestions that woody Saxifragales may be closely related to Dipsacales (e.g., Takhtajan, 1987). This idea gains support from analyses of the chloroplast gene *rbc*L (Chase et al., 1993; Olmstead et al., 1992, 1993), which imply that *Escallonia* is located among Asteridae s.l. in the vicinity of Dipsacales and Araliales. Pittosporaceae are included as a representative of the Araliales/Asterales clade. These choices are also supported by a morphological cladistic analysis (Hufford, 1992).

Whether Dipsacales are monophyletic has been uncertain, because unique morphological characters have not been identified (Donoghue, 1983). In our parsimony analyses (see below) taxa of Dipsacales attached to the presumed outgroups by a branch along which there is an inferred change in phyllotaxy (char. 2), and possible changes in stamen attachment (char. 15) and endosperm development (char. 29). The resulting networks were rooted along this branch. The fact that the presumed ingroup and outgroup taxa are attached along a single branch provides support for the monophyly of Dipsacales; however, our sample of outgroups is so limited that the test is clearly weak. Dipsacales are found to be monophyletic in several large analyses of *rbc*L (Chase et al., 1993; Olmstead et al., 1992, 1993), but not in a smaller study that included a better sample of Dipsacales *rbc*L sequences (Donoghue et al., 1992), nor in an analysis of restriction site data from the cpDNA inverted repeat (Downie and Palmer, 1992).

Taxa were scored for 36 potentially informative characters (25 binary and 10 multistate), which would require a minimum of 50 state changes (steps) in the absence of homoplasy (Tables 11, 12). Of these, 10 characters reflect aspects of vegetative morphology (including stem anatomy; DeVos 1951), secondary chemistry (Bohm and Glennie, 1971), and chromosomes (Sax and Kribs, 1930). In addition to standard floral features, such as the number, size, fusion, and symmetry of parts (see Donoghue, 1983; Fritsch, 1891; Fukuoka, 1972; Hara, 1983; Weberling, 1957), reproductive characters were obtained from detailed studies of the inflorescenses (Troll and Weberling, 1966), floral anatomy (Fukuoka, 1972; Wilkinson, 1949), nectaries (Wagenitz and Laing, 1984), pollen grains (Bohnke-Gutlein and Weberling, 1981; Donoghue, 1985), tapetum development (Weberling and Hildenbrand, 1986), and embryo sac development (Maheshwari, 1946).

Seven of the 10 multistate characters were treated as unordered in our primary analysis, and three as ordered (chars. 7, 20, 23). Truncated monotelic inflorescences (char. 7), characterized by abortion of the terminal flower, are considered transitional between monotelic and polytelic forms based on the arguments of Weberling (1989). Exine "structure" (char. 20) reflects both the presence or absence of a tectum and of columellae. We suppose that one change is involved in the transition between semitectate and tectate grains, and that there is a second change in the presence/size of the columellae in tectate forms (Bohnke-Gutlein and Weberling, 1981; Donoghue, 1985). Likewise character 23 involves changes in both style length and stigma lobing. Our coding puts one step between an elongate style with a lobed stigma and the other two conditions: elongate/capitate and short/lobed. Thus, a transition between the latter two states requires two steps: one in style length and one in stigma lobing. Coding 3-state characters of this type as two binary characters yields the same ordering of the three conditions. Although it results in a loss of information, we note that the basic conclusions highlighted below were also obtained when all multistate characters were unordered.

Some characters are unknown, inapplicable (e.g., nectary number when nectaries are lacking), or otherwise uninterpretable in one or more taxa. These are scored as "?" in the matrix. Polymorphism coding (e.g., 0/1) was used when two (or more) states are known within a taxon (e.g., actinomorphic and zygomorphic corollas) or even within individual plants (e.g., variation in vessel perforations during ontogeny), and when evidence is lacking as to which state is ancestral in the group (e.g., based on a previous phylogenetic study of the group in question). Subdivision of polymorphic taxa was considered undesirable because the monophyly of terminal taxa was not at issue, and because it appeared that in no case would it have been necessary to divide a taxon into more than two taxa (circumstances that might result in the difficulties highlighted by Nixon and Davis, 1991).

Results. Six most parsimonious trees of 64 steps were obtained (CI=0.8; RI=0.85). The strict consensus of these trees is shown in Figure 5. This tree also happens to be one of the most parsimonious solutions, and therefore is used to show the position of character changes.

The main phylogenetic conclusion of this analysis is that Caprifoliaceae in its standard sense is paraphyletic, with the other families of Dipsacales nested within it. The primary division is not between the traditional families, but rather between a *Viburnum*/*Sambucus*/*Adoxa* clade and a clade which includes the

TABLE 12. Caprifoliaceae/Dipsacaceae/Valerianaceae Matrix (*=characters with notes; ?=missing; a={01}; b={12}; c ={012}; d={02}).

		*		*			
	* * *	***1	** *	* *2	** *	* **3	* ***
	12345	67890	12345	67890	12345	67890	12345
Adoxa	11111	?00?1	10201	01000	102b0	??110	40?00
Sambucus	a1111	00011	100?1	01100	102b0	01110	30000
Viburnum	010a0	00011	10a?1	00100	10213	01010	3000a
Leycesteria	01010	12000	2a301	00011	2a020	10010	2011?
Lonicera	0101a	12010	2a3a1	00011	200c0	10010	20110
Triosteum	11010	?2000	21301	00011	20021	?1010	40110
Symphoricarpos	0101a	1b010	2a301	000?1	20a22	11010	40110
Weigela+ *Diervilla*	01010	11000	21311	00?12	21000	10010	10010
Linnaea	01010	11100	2a311	10?11	2?0b2	11010	50?11
Dipelta	01010	11100	21311	10?11	21022	11010	50?11
Kolkwitzia+ *Abelia*	01010	11100	21311	10011	21012	11010	50011
Valerianaceae	11a11	?10d?	21311	10011	21012	11011	51???
Dipsacaceae	11a11	?1?2?	21311	10011	210??	1?011	51???
Alseuosmiaceae	00010	0?00?	201?a	00??1	10100	?0??0	2????
Pittosporaceae	00001	??00?	000?0	0??0?	00100	0?000	00???

1: Woody is probably ancestral in *Sambucus*; the first Valerianaceae and Dipsacaceae were probably perennial herbs, with limited cambial activity (as in *Nardostachys*). **3:** The ancestral condition in Valerianaceae is probably simple (as in *Nardostachys*). **5:** The perforations in *Lonicera* and *Symphoricarpos* are mostly simple, but scalariform perforations are sometimes present near the primary xylem (DeVos, 1951). **7:** A terminal flower is occasionally produced in *Diervilla* (which is therefore facultatively monotelic), but apparently not in *Weigela* (Weberling, 1989). **8:** The scoring of Dipsacaceae depends on the interpretation of the epicalyx. **9:** Unmodified sepals may be ancestral in Valerianaceae (as in *Nardostachys*). **10:** A single trace occurs in some *Diervilla* and *Lonicera*, where it is presumably derived. **11:** An elongate tube is found in several species of *Viburnum*, but this is presumed to be derived within the genus (Donoghue, 1983). **12:** Nectaries are massive in *Weigela*/*Diervilla* and some species of *Abelia* (Wagenitz and Laing, 1984). **15:** The degree of attachment of the stamens varies within Alseuosmiaceae (Gardner, 1978). **17:** Introrse anthers are sometimes observed in *Sambucus* (Fukuoka, 1972). **19:**. Pollen grains are intermediate in size in Alseuosmiaceae (Erdtman, 1971); wide variation is reported in *Symphoricarpos*. **20:** Taxa scored 1 and 2 also have supratectal spines; however, these are lacking in some grains of *Triosteum*, *Symphoricarpos*, and *Abelia* (Donoghue, 1983; Hara, 1983). **21:** Elongation of the ovary is associated with a great increase in the number of ovules/seeds in *Weigela* and *Diervilla*. In *Kolkwitzia* the ovary is globose at the base, with a distinct neck above; *Linnaea* shows an intermediate condition. **22:** Four carpels are sometimes found in *Leycesteria*; in *Linnaea* there are usually three carpels, but occasionally four. **25:** The presence of three carpels in *Triplostegia* suggests that the pseudomonomerous ovary in Dipsacaceae was derived from the condition in Linnaeeae and Valerianaceae. **26:** Free dorsal traces are lacking in *Triosteum*, and the marginal bundles are not recessed (as they are in other taxa scored 1); however, lateral traces are present. **28:** Information on embryo-sac development is limited in Alseuosmiaceae; however, the *Polygonum*-type occurs in *Escallonia* (a presumed close relative). **29:** Information on the endosperm of Alseuosmiaceae is limited, but nuclear development is reported for *Escallonia*. **31:** The fruit of *Linnaea* is intermediate between a drupe and an achene (dry covering, one seeded); the fruit of *Kolkwitzia* is sometimes described as a nut (hardened endocarp, dry covering, one seeded). **33:** The flavonols are kaempferol and quercetin; flavones are apigenin and luteolin (Bohm and Glennie, 1971). **34:** 0=1.2-2 cubic microns, 1=≤0.5 cubic microns (Sax and Kribs, 1930). **35:** Pittosporaceae: X=12; Valerianaceae: X=7-12 (mostly 9); Dipsacaceae: X=5-10 (perhaps originally 9).

Caprifoliaceae s.s., the Valerianaceae, and the Dipsacaceae.

Adoxa is linked with *Sambucus* based on compound leaves (char. 3), simple vessel perforations (char. 5), extrorse anthers (char. 17), and *Adoxa*-type embryo sacs (char. 28: the *Adoxa*-type embryo sac is tetrasporic and 8-nucleate). This clade is connected to *Viburnum* by reduced calyx lobes (char. 9) with one vascular trace (char. 10), rotate corollas (char. 11), semitectate-reticulate pollen grains (char. 20), short styles (char. 23-2), and drupe fruits (char. 31-3).

The genera of Caprifoliaceae s.s. are united with Valerianaceae and Dipsacaceae by possession of long, zygomorphic corolla tubes (char. 12) with nectary tissue of unicellular hairs (char. 13-3), large pollen grains with supratectal spines (char. 19), fully inferior ovaries (char. 21-2), capitate stigmas (char. 23), and reduced carpel vasculature (char. 26). The best supported group within this clade includes the genera of Linnaeeae and the Valerianaceae plus Dipsacaceae. These groups are united by reductions to one nectary (char. 14), four stamens (char. 16), and 8 chromosomes (char. 35). In addition, two of the three carpels abort (leaving a single-seeded carpel occupying half of the ovary; char. 25-2) and the mature fruit is an achene (char. 31-5).

The view that the pseudomonomerous ovary of Dipsacaceae is a modification of the condition seen in Linnaeeae and Valerianaceae is supported by the 3-carpellate gynoecium of *Triplostegia* (the likely sister group of Dipsacaceae s.s.). Valerianaceae and Dipsacaceae are united by simple vessel perforations, monoterpenoids, reduced endosperm, and (usually) modified calyx lobes.

Discussion. As in our other examples, distinctive and more recently evolved lineages of herbs have been elevated to family rank, leaving behind a paraphyletic group of woody plants. Moreover, the paraphyletic Caprifoliaceae show greater diversity in morphology than the segregate families. This is especially clear in the case of the gynoecium (which varies in the number, abortion, and vasculature of the carpels and ovules), as well as in fruit types (capsules, berries, achenes, fleshy and dry drupes). Our analysis implies that many of the features considered to be distinctive of Valerianaceae and Dipsacaceae (ovary development, reduced stamen number) actually evolved earlier, in their common ancestor with Linnaeeae.

Our morphological results are basically congruent with those based on molecular evidence (Chase et al., 1993). In a preliminary analysis of *rbc*L sequences (Donoghue et al., 1992) *Adoxa* and *Sambucus* were linked and were related in turn to *Viburnum*, while *Lonicera* plus *Symphoricarpos* were joined with Valerianaceae and Dipsacaceae. Although these two clades were not linked directly in the most parsimonious trees, trees with the Dipsacales monophyletic required just one extra step. The genera of Caprifoliaceae did not form a clade, and trees in which they are monophyletic cost at least 14 steps.

Downie and Palmer's (1992) analysis of restriction site characters from the cpDNA inverted repeat yielded similar results. *Viburnum* was linked with genera of Caprifoliaceae s.s., and the latter were seen to be paraphyletic, with Valerianaceae and Dipsacaceae nested within. *Kolkwitzia*, the one genus of Linnaeeae included in their analysis, was linked directly with *Valeriana*.

Many of our conclusions were anticipated based (presumably) on overall similarity. For example, according to Cronquist (1981, pp. 1002-1003): "The Caprifoliaceae are obviously the most archaic family in the Dipsacales. The Valerianaceae appear to take their origin directly from the Caprifoliaceae. The Dipsacaceae are a little more removed, but evidently of the same ancestry." In support of the same view, Takhtajan (1980) cited Wilkinson (1949), who put the matter even more precisely: "The similarities between the Valerianaceae and the Linnaeeae are too significant to be considered as due simply to parallel development. The two groups are closely related."

Although the relationships of *Adoxa* have been much more controversial, several earlier authors suggested a direct connection to *Sambucus*. Takhtajan (1980) cited Eichler (1875) and Hallier (1912) in support of this idea, quoting Hallier to the effect that *Adoxa* is simply a reduced *Sambucus*. Thorne (1983, 1992a, 1992b) formally adopted this view in recognizing an expanded Adoxaceae (including *Sambucus* and *Viburnum*), but this was influenced by Donoghue's (1983) phylogenetic analysis.

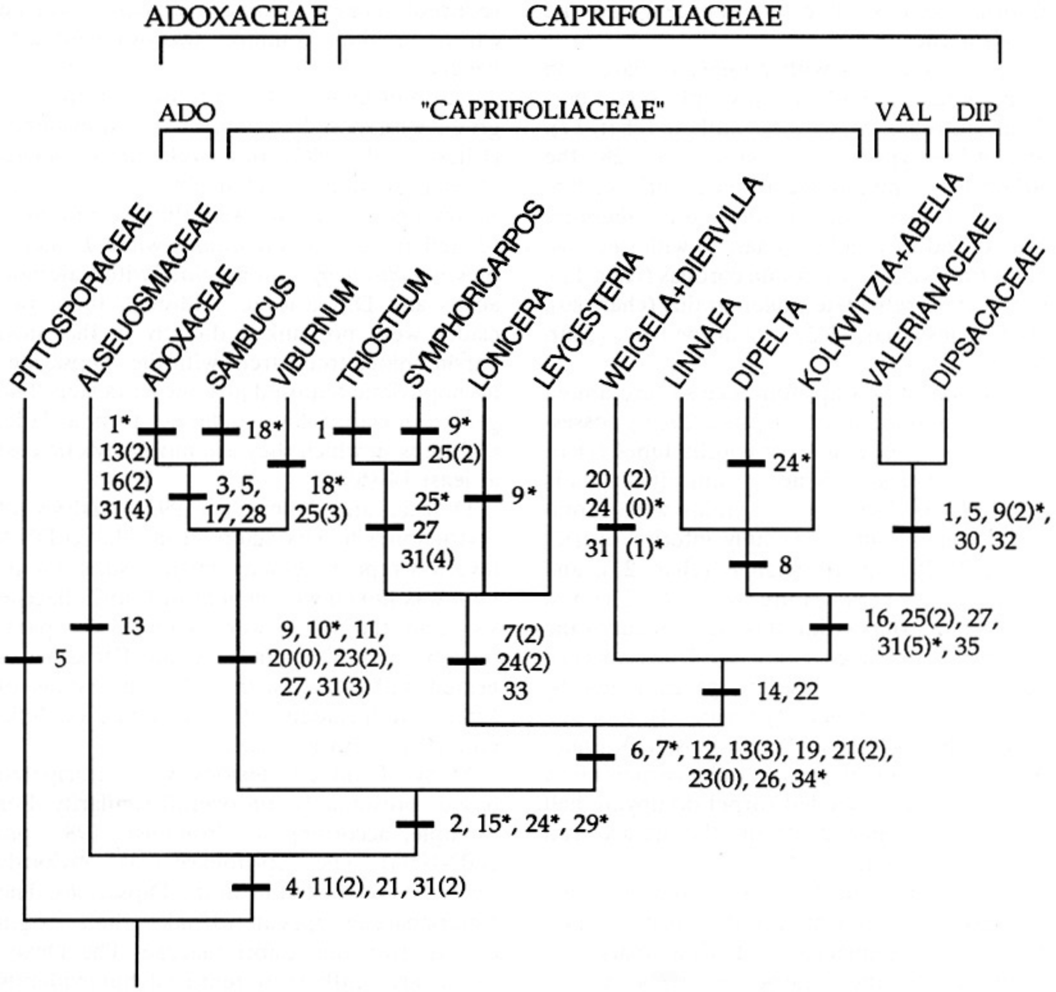

Fig. 5. Representative tree (64 steps) resulting from analysis of Caprifoliaceae/Dipsacaceae/Valerianaceae; CI=0.80. Topology of this tree is identical to that of the strict consensus of the 6 trees resulting from analysis. * = one or more alternative placements are equally parsimonious.

Some of our results are more surprising. For example, *Symphoricarpos* has usually been allied with Linnaeeae (e.g., Hara 1983; Table 10), yet it is linked in our analysis with *Triosteum*, and in turn with *Lonicera* and *Leycesteria* of Caprifolieae. The connection to *Triosteum* was suggested by Donoghue (1985) based on pollen morphology and, as noted above, *Symphoricarpos* is strongly linked with *Lonicera* based on *rbc*L sequences (Donoghue et al., 1992).

A number of taxonomic changes are needed to reflect the best-supported phylogenetic relationships represented in Figure 5. In particular, it is misleading to continue to recognize Caprifoliaceae in its traditional sense. Instead, names are needed to reflect that some Caprifoliaceae are more closely related to *Adoxa* and others are more closely related to Valerianaceae plus Dipsacaceae. Accordingly, we propose the recognition of two newly defined taxa, which, in keeping with tradition, are considered families: Adoxaceae and Caprifoliaceae (Fig. 5). Pending further study of the monophyly of Dipsacales, these are provisionally retained in that taxon. Other new taxa will be needed to reflect accurately the hypothesized relationships within these families; for example, the *Sambucus-Adoxa* clade (Adoxoideae of Thorne, 1983, 1992a, 1992b) and the clade comprised of Linnaeeae, Valerianaceae, and Dipsacaceae.

The name Adoxaceae is here defined to include the most recent common ancestor of *Viburnum*, *Sambucus*, *Adoxa*, and all of its descendants, whether recent or extinct (a "node-based" phylogenetic definition; de Queiroz and Gauthier, 1990, 1992). The choice of the name Adoxaceae for this family is dictated by priority at the family level (Table 19). Adoxaceae also has priority from a phylogenetic perspective (de Queiroz and Gauthier, 1990), as it was the first name associated with the clade/ancestor in question (Donoghue, 1983; Thorne, 1983). This taxon can be diagnosed by the synapomorphies shown in Figure 5, but we draw special attention to rotate corollas, semitectate-reticulate pollen grains, short styles with separate stigma lobes, 3-5 carpellate gynoecia, and drupe fruits. Although these features are obviously not unique to this group, and in some cases are modified within the group, they do provide evidence of monophyly in the context of presumably related plants.

The name Caprifoliaceae is redefined to refer to the most recent common ancestor of plants previously considered to be Caprifoliaceae s.s. (or subfamily Caprifolioideae sensu Hara, 1983) as well as those assigned to Valerianaceae and Dipsacaceae, and all of the descendants of that ancestor. Note that under this circumscription the Valerianaceae and the Dipsacaceae are no longer recognized as taxa at the family level. However, inasmuch as these appear to be clades, they presumably will continue to be recognized as taxa (at some level in the hierarchy). The newly circumscribed Caprifoliaceae can be diagnosed by several presumed synapomorphies: tubular, generally zygomorphic corollas, large pollen grains with supratectal spines, fully inferior ovaries, capitate stigmas, and reduced carpel vasculature.

MORACEAE AND URTICACEAE

Taxa and characters. Thirteen representative genera of Urticales were scored for seventeen characters (Tables 13-15). *Tilia* (Tiliaceae, Malvales) was included as an outgroup because it is likely that the Urticales were derived from a generalized member of Malvales (see, for example, Weddell, 1856-7; Hallier, 1903; Bessey, 1915; Thorne, 1973b, 1976, 1983; Stebbins, 1974; Berg, 1977, 1989; Dahlgren, 1980, 1983). Characters that may indicate a close relationship between these orders are presence of alternating fibrous and nonfibrous layers in the phloem (i.e., stratified phloem); extruded nucleoli in the sieve-tube elements; often palmately veined, alternate, and stipulate leaves; and patterns of variation in the inflorescences, fruits, seeds, and embryos (see also Berg, 1977; Thorne, 1973b). Berg (1977, p. 371) stated that the "affinities of the Urticales with the Malvales are closest between the Ulmaceae and Tiliaceae, the least derived families of the orders." In contrast, some taxonomists, e.g., Cronquist (1968, 1981, 1988) place the Urticales in the Hamamelidae. We note that the use of *Ulmus* as a functional outgroup does not change in-group structure.

All characters were readily divisible into discrete states. A few taxa, however, are polymorphic for particular features (see Table 15, notes). Character 2 (laticifer condition) is multistate; it was treated as an ordered, linear transformation series (see Tables 14, 15).

TABLE 13. Moraceae/Urticaceae Taxa*

Moraceae s.s. (Moraceae s.l. includes Cecropiaceae; some systematists also include Cannabaceae.)

- *Artocarpus*
- *Brosimum*
- *Dorstenia*
- *Fatoua*
- *Ficus*
- *Morus*

Cecropiaceae

- *Cecropia*
- *Poikilospermum*

Cannabaceae

- *Cannabis*

Urticaceae

- *Pilea*

Ulmaceae

- Celtidoideae
    - *Celtis*
- Ulmoideae
    - *Ulmus*

Tiliaceae

- *Tilia* (OG)

*Classification based on Thorne (1992) and Cronquist (1981)

TABLE 14. Moraceae/Urticaceae Characters

1.	HABIT: woody (0), herbaceous (1)
2.	LATICIFERS: absent (0), present throughout (1), present in bark (2) (ordered)
3.	LATEX: milky (or absent) (0), mucilaginous (1)
4.	CYSTOLITHS: absent (0), present (1)
5.	CYSTOLITH TYPE: globose (0), elongate (1)
6.	WOOD FIBERS: monomorphic, pits radial only (0), dimorphic, pits radial and tangential (1)
7.	VESSEL ELEMENTS: lignified (0), unlignified (1)
8.	STAMENS: more or less straight (0), incurved in bud (explosive pollen dehiscence) (1)
9.	STIGMAS: 2 (or more) (0), one (gynoecium pseudomonomerous) (1)
10.	PLACENTATION: apical (or ovary multilocular) (0), basal (1)
11.	OVULES: anatropous, amphitropous, hemitropous, or campylotropous (0), more or less orthotropous (1)
12.	INFLORESCENCES: cymose; axes slender (0), highly modified, and discoid, cup-like, or a syconium; axes thichened, expanded (1)
13.	FLOWERS: conspicuous (0), reduced (1)
14.	OVARY: multilocular, placentation axile (0), unilocular, placentation apical or basal (1)
15.	STAMENS: more or less numerous (0), 5 or less (1)
16.	FLOWERS: perfect (0), imperfect (1)
17.	PROPHYLLAR BUDS: not well developed on shoot (0), at least one prophyll basal on shoot, even if sylleptic, and with a branch or prominent bud developed in its axil (1); (P. F. Stevens, pers. comm.)

Results. The initial PAUP analyses resulted in the discovery of four equally parsimonious trees of 22 steps and a CI of 0.82 (0.79 when characters uniform within the ingroup are disregarded; RI=0.83), which differed only in the relative positions of *Morus*, *Fatoua*, and *Cannabis*. *Fatoua* was sometimes linked with *Cannabis* on the basis of the herbaceous habit (a probable parallelism) and sometimes with *Morus* due to its inflexed stamens (a diagnostic feature of the tribe Moreae). The analysis was re-run with character 1 (habit type) deleted, which resulted in the discovery of a single most parsimonious tree (Fig. 6) of 19 steps and a consistency index of 0.90 (0.88 when characters uniform within ingroup are disregarded; RI = 0.91), which was identical to one of the cladograms discovered in the initial analyses. This tree is quite similar to the cladogram resulting from a preliminary cladistic analysis of the order by Humphries and Blackmore (1989). We should note that our analyses differ from those of Humphries and Blackmore in that we included *Ulmus* and *Celtis* as separate taxa (not combined as "Ulmaceae"), included *Cannabis* (as representing Cannabaceae), and considered the distinctive ± herbaceous genus *Fatoua* separately from remaining members of Moreae (in our analyses represented by *Morus*). We scored a few characters differently, e.g., *Cannabis* is considered to have laticifers as well as latex (Metcalfe, 1966), Urticaceae are considered to possess reduced laticifers (see Miller, 1971), and cystoliths are scored as present in *Ulmus* and *Celtis* (W. Judd, pers. observations). In addition, we added the character of prophyllar bud development (Table 14).

The cladogram resulting from our analysis (Fig. 6) indicates that Moraceae, as variously delimited (see Engler, 1889; Lawrence, 1951; Cronquist, 1981; Thorne, 1976; Berg, 1989) are paraphyletic. Cecropiaceae, as currently recognized (Berg, 1978, 1989; Cronquist, 1981), are also paraphyletic. Urticaceae are hypothesized to be monophyletic (see also Friis, 1989).

Our results indicate that *Pilea* (Urticaceae) is the sister group of *Poikilospermum* (an isolated genus in the Cecropiaceae; see Berg, 1989) on the basis of several anatomical features (chars. 6, 7). These two groups form the sister-clade to *Cecropia* (representative of the remainder of Cecropiaceae; see Berg, 1989). These three genera form a well supported clade, and are linked by laticifers limited to the bark (char. 2-2), more or less mucilaginous latex (char. 3), gynoecium with a single stigma (i.e., pseudomonomerous; char. 9), basal placentation (char. 10), and orthotropous ovules (char. 11).

TABLE 15. Moraceae/Urticaceae Matrix (*=characters with notes; a={0/1})

		*		
	*** *	***1	* *	
	12345	67890	12345	67
Tilia	0000?	00000	00000	00
Ulmus	00010	00000	00111	00
Celtis	00010	00000	00111	11
Cannabis	11010	00000	00111	11
Artocarpus	01010	00000	00111	11
Morus	01010	00100	00111	11
Dorstenia	01010	00000	01111	11
Brosimum	01010	00000	01111	11
Ficus	01010	00000	01111	11
Cecropia	0210?	00011	10111	11
Poikilospermum	02111	11011	10111	11
Fatoua	11010	00100	00111	11
Pilea	1211a	11111	10111	11

1: The ancestral condition in *Dorstenia* is frutescent; see Berg (1977, fig. 1) for evolutionary trends in habit within this genus. Although *Pilea* is herbaceous, several genera of Urticaceae are woody, e.g., *Gyrotaenia*, *Urera*, *Boehmeria* (some species), *Dendrocnide* (a segregate of *Laportea*). **2:** Laticifers are found in both *Cannabis* and *Humulus* (Cronquist, 1981; Metcalfe, 1966). Cronquist (1981) reported that laticifers are lacking in *Fatoua*; however, older stems and petioles exude a milky latex when cut (W. Judd, pers. observation). Laticifers are known from a few genera of Urticaceae, e.g., *Urtica*, *Dendrocnide*, *Laportea*, *Urera*, are restricted to the bark (Metcalfe and Chalk, 1950; Miller, 1971; Cronquist, 1981; Humphries and Blackmore, 1989); this condition is considered to be ancestral within Urticaceae (out-group comparision), see scoring of *Pilea* as state 2 above. Scoring *Pilea* as 0 for this character results in no change in topology of the resulting cladogram (see text). **3:** In *Cannabis* the contents of the laticifers are "in the form of a yellowish-brown mass" (Metcalfe, 1966, p. 5). **5:** Cystoliths are lacking in *Cecropia* (W. Judd, pers. observation; Berg, 1978). Cystolith form is diverse in Urticaceae, with spherical, bacilliform, fusiform (curved to straight), stellate, and vermiform types (Miller, 1971). **6:** Scoring based on Humphries and Blackmore (1989). **7:** Scoring based on Humphries and Blackmore (1989); Bonsen and ter Welle (1983) argued that owing to the possession of unlignified vessel elements *Poikilospermum* should be excluded from the Moraceae and placed close to *Nothocnide* in the Urticaceae. **8:** The inflexed stamens of *Celtis laevigata* (Cuellar, 1967) are considered an independently acquired condition. According to Berg (1978, p. 42, 43) "members of [*Poikilospermum*] subg. *Poikilospermum*, have more or less inflexed stamens, which apparently straighten gradually at anthesis," and this condition "should be regarded as distinct from those bending outward elastically." **9:** A few members of *Artocarpus*, *Dorstenia*, and *Ficus* have flowers with the gynoecium reduced, with only a single stigma; the possession of 2 stigmas/styles is considered ancestral in these genera. **10:** In *Fatoua* the ovule appears to be basal due to the lateral/basal attachment of the style. **12:** Inflorescences with expanded axes also occur in some Moreae (Berg, 1989). **14:** The ovary is sometimes bilocular in *Ulmus* (Elias, 1970). It is bilocular in *Morus*, each locule with a single ovule; not several ovules as in most Tiliaceae.

Poikilospermum and *Pilea* share elongate cystoliths (and the elongate form of these crystals may be synapomorphic); crystals have been lost in *Cecropia*.

Relationships among the genera of Moraceae are less clear, although *Dorstenia*, *Brosimum*, and *Ficus* form a clade based on their highly modified inflorescences (char. 12; see Fig. 6, and discussion in Humphries and Blackmore, 1989). Berg (1977, 1989), however, considered inflorescences with thickened axes, i.e., discoid, cup-like, synconia, etc., to have evolved independently in several lineages (see Berg, 1989, figs. 11.2 & 11.3). *Fatoua* and *Morus* are joined on the basis of their inflexed/explosive stamens (char. 8), a feature that presumably evolved independently in the Urticaceae (see also Berg, 1989, fig. 11.1).

Ulmus and *Celtis* (representatives of Ulmaceae s.l.) constitute the two basal lineages within Urticales (among included taxa; Fig. 6). Thus, Ulmaceae, as usually circumscribed, appear to be paraphyletic. *Celtis* is united with genera usually placed in Moraceae, Cecropiaceae, or Urticaceae (Fig. 6) by the presence of consistently imperfect flowers (char. 16), and axillary branches and/or inflorescences with at least one well developed prophyllar bud (char. 17). Members of the Moraceae/Cecropiaceae/Urticaceae clade show the development of laticifers (char. 2; reduced in some).

It is clear that the order is monophyletic, as indicated by the following synapomorphies: cystoliths (char. 4); reduced, inconspicuous flowers (char. 13); with five or fewer stamens (char. 15); unilocular (or rarely 2-locular; possibly a retained plesimomorphic condition) ovaries (char. 14) with apical to basal placentation.

Discussion. Our cladogram gives strong support to the classification of Thorne (1983), who on phenetic grounds treated the genera of Moraceae, Cecropiaceae, and Urticaceae within a single broadly defined family: Urticaceae. Thorne had earlier (1976) maintained Moraceae, but transfered *Cecropia*, *Poikilospermum* and relatives to the Urticaceae, as subfamily Cecropioideae, stressing the numerous characters shared by these taxa (see Fig. 6); similar classifications had been proposed by Corner (1962) and Chew (1963). This alternative, however, does not remove the problem of the possible paraphyly of the Moraceae s.s. Our results also reinforce the analysis of the Urticales conducted by Humphries and Blackmore (1989).

We support their conclusion that the "Moraceae is not supported as monophyletic on the characters analyzed" (Humphries & Blackmore, 1989, p. 276) and that Cecropiaceae and especially *Poikilospermum* are more closely related to Urticaceae than to Moraceae.

The recognition of Cecropiaceae (see Berg, 1978, 1989; Cronquist, 1981; Thorne, 1992a, 1992b), as well as Urticaceae s.s. (see Engler, 1889; Miller, 1971; Cronquist, 1981; Friis, 1989) cannot be justified from a cladistic standpoint. The recognition of Urticaceae as a family leads to a paraphyletic Moraceae, while the recognition of both Urticaceae and Cecropiaceae as families leads to a metaphyletic Moraceae (see Fig. 6; for a discussion of metaphyly see Mishler & Brandon, 1987). Cecropiaceae, if it includes *Poikilospermum* (as circumscribed by Berg, 1978), is paraphyletic (see Fig. 6; and Humphries & Blackmore, 1989, fig. 14.1). Berg (1989, p. 215) also noted this problem, and stated that "the delimitation of the family is doubtful only with respect to the Asian-Australasian genus *Poikilospermum* that deviates in several features (e.g., the elongate = 'Urticaceous' cystoliths) from the group of African and American genera. Anatomical data . . . suggest that the position of *Poikilospermum* is separate from the other five genera and closer to Urticaceae." Bonsen and ter Welle (1983) provided a detailed discussion of these anatomical features.

Support for the derivation of Urticaceae from within Moraceae also comes from anatomical and developmental studies. Aborted vascular bundles in gynoecia of *Laportea canadensis* and *Urtica gracilis* suggest that the unicarpellate ovary has been derived through abortion of a second (and anterior) carpel (Bechtel, 1921). The basal ovule of the Urticaceae, likewise, has apparently been derived from the more or less apical ovule of the Moraceae; in *Boehmeria cylindrica* the vascular bundle supplying the ovule ascends the carpel wall for a short distance and later reverses direction to enter the ovule at the base of the ovary (Bechtel, 1921; Miller, 1971).

It is of interest that herbs (or near herbs) have evolved several times within the "Moraceae". *Fatoua*, which is herbaceous, and has flowers with incurved/explosive stamens, and a gynoecium in which one carpel is extremely reduced, is especially urticaceous in appearance! Gynoecium reduction also has occurred in several lineages. It is common within Moraceae for the two stigmas to be unequal in length; e. g., in *Artocarpus, Dorstenia, Ficus, Milicia*, *Fatoua*, and sometimes the second stigma has been completely lost (Berg, 1989).

Although the elucidation of relationships within the Ulmaceae s. l. was not a goal of our investigation, the results of these analyses support the view of Grundzinskaja (1967) that the Celtidoideae and Ulmoideae each should be recognized at the familial level. The Ulma-

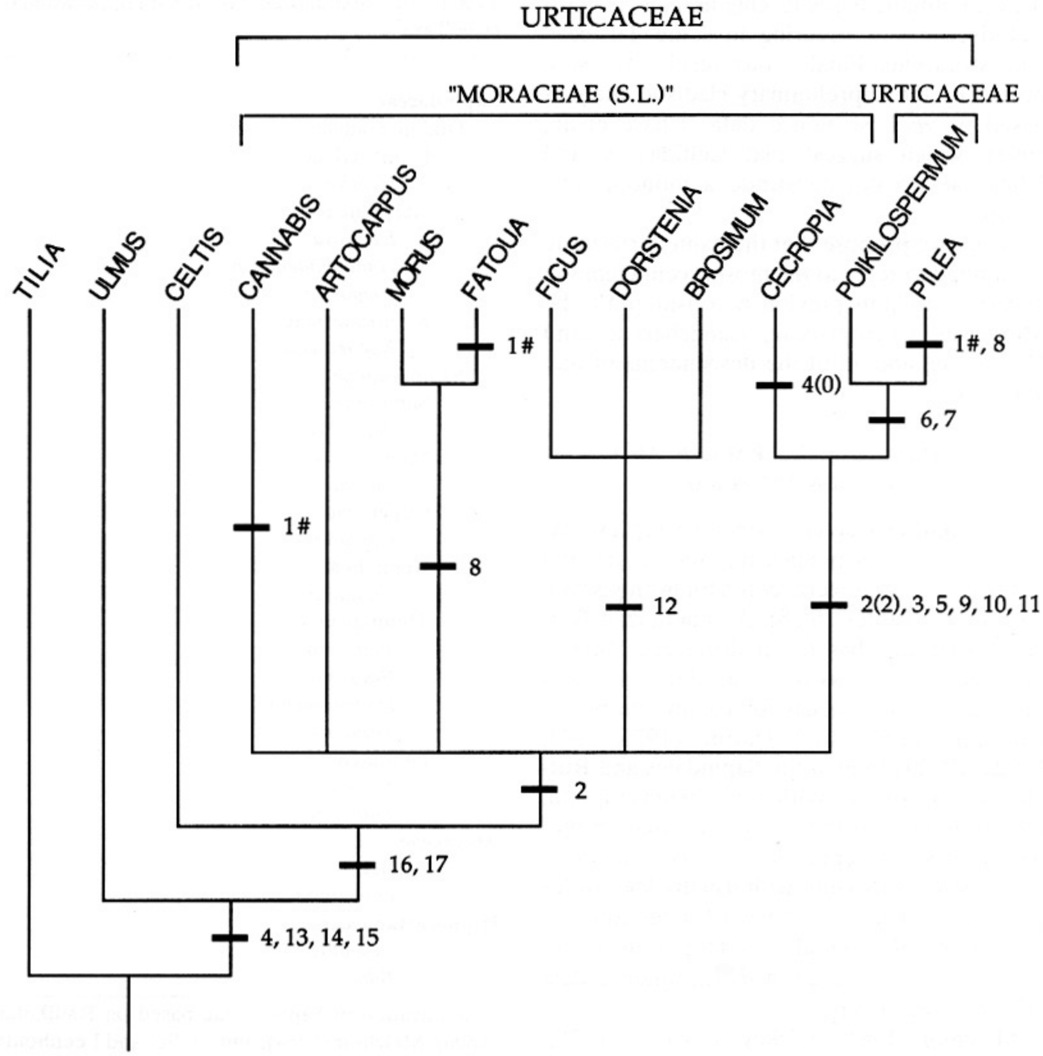

Fig. 6. Single shortest tree (22 steps) obtained in analysis of Moraceae/Urticaceae; CI = 0.90. # = character deleted from analysis (and merely mapped onto cladogram).

ceae s.s. and Celtidaceae differ in an impressive list of features, e.g., the pattern of leaf venation (Grundzinskaja, 1967) and vernation (Terabayashi, 1991), floral morphology and sexuality (Grundzinskaja, 1967), fruit type (Grundzinskaja, 1967; Chernik, 1980), embryo shape (Grundzinskaja, 1967), palynology (Erdtman, 1971), wood anatomy (Tippo, 1938), flavonoid chemistry (Giannasi, 1978), and chromosome number and morphology (Oginuma et al., 1990); see Cronquist (1981) for a discussion of many of these citations. It is especially noteworthy that for most of these features, the condition present in *Celtis* (and Celtidaceae) is more similar to that found in the Moraceae and/or Urticaceae s.s. than that found in *Ulmus* and relatives (i.e., Ulmaceae s.s.). Some of these similarities, in addition to those included in our analyses, likely are synapomorphic, e.g., drupaceous fruits and curved embryos. Asymmetric (or oblique) leaf bases, often considered to be a diagnostic feature for Ulmaceae s.l., may be of little phylogenetic significance. This feature is clearly homoplastic, with oblique bases lacking in many tropical Celtidaceae and occuring in some Tiliaceae and Moraceae. Finally, our results are supported by those preliminary cladistic analyses based on *rbc*L sequence data (Chase et al., 1993), which suggest that Celtidaceae and Ulmaceae do not constitute a monophyletic group.

Thus, we propose that the name Urticaceae be defined to refer to the most recent common ancestor of plants previously considered to be Moraceae, Cecropiaceae, Cannabaceae, and Urticaceae, and all of the descendents of that ancestor.

SAPINDACEAE, ACERACEAE, AND HIPPOCASTANACEAE

Taxa and characters. Nineteen representative genera of Sapindaceae, Aceraceae, and Hippocastanaceae were scored for twenty-seven characters (Tables 16-18). A generalized Rutales outgroup, based on Rutaceae, Simaroubaceae, Burseraceae, and Meliaceae, was included in the analysis for rooting purposes. Cronquist (1981) and Thorne (1976, 1983, 1992a, 1992b) treated the Sapindales and Rutales as one order. With this circumscription, the group likely is monophyletic based on pinnate leaves, a receptacular nectary disk, and a syncarpous gynoecium with usually few ovules per carpel. The monophyly of a broadly circumscribed Rutales also is supported by recent analyses based upon *rbc*L sequence data (Chase et al., 1993).

Melchior (1964), Hickey & Wolfe (1975), Dahlgren (1983), and Tahktajan (1980) restricted the Sapindales to the Sapindaceae, Aceraceae, and Hippocastanaceae, plus several anomalous genera that are treated as segregate families. The selection of one or a few of these odd genera or of the specialized Anacardiaceae (which Melchior, 1964, and Dahlgren, 1983, place in the Sapindales) as immediate outgroups cannot be justified based on our rudimentary knowledge of phylogenetic relationships within Rutales.

TABLE 16. Sapindaceae/Aceraceae/Hippocastanaceae Taxa*

- **Sapindaceae**
  - Dodonaeoideae
    - Doratoxyleae
      - *Hypelate*
    - Harpullieae
      - *Delevaya*
      - *Handeliodendron*
      - *Ungnadia*
    - Koelreuterieae
      - *Koelreuteria*
  - Sapindoideae
    - Sapindeae
      - *Sapindus*
    - Melicocceae
      - *Talisia*
    - Cupanieae
      - *Cupania*
    - Nephelieae
      - *Euphoria*
    - Thouinieae
      - *Athayana*
      - *Bridgesia*
      - *Diatenopteryx*
      - *Thouinia*
    - Paullineae
      - *Serjania*
      - *Thinouia*
- **Aceraceae**
  - *Acer*
  - *Dipteronia*
- **Hippocastanaceae**
  - *Aesculus*
  - *Billia*

*Classification of Sapindaceae based on Radlkofer (1896), Melchior (1964), and Muller and Leenhouts (1976).

Owing to wide variation in a few characters among Rutales, this taxon was sometimes scored as polymorphic or as "?" (see Table 18). Initially, all nine multistate characters were run unordered. In most cases, the preliminary analyses verified a hypothesized character-state ordering (see Table 17), which was used in subsequent analyses. Four characters, i.e., 2, 15, 24, and 25, were left unordered in subsequent analyses. A few characters that we considered initially were deleted because they were too variable within ingroup genera and/or outgroup families, or because they appeared to be functionally correlated with other included features. Some of these (i. e., multiseriate vs. uniseriate wood rays; intercostal venation admedially ramified; leaf margins entire vs. simple-toothed vs. compound-toothed to lobed; petal veins three but running closely parallel

TABLE 17. Sapindaceae/Aceraceae/Hippocastanaceae Characters

1.	PHYLLOTAXY: alternate (0), opposite (1)
2.	LEAF TYPE: pinnately organized (0), palmately compound (1), palmately organized (2)
3.	LEAF TYPE: not paripinnate (incl. simple) (0), paripinnate (1)
4.	PETIOLE: cylindric or tumid at base (0), with an adaxial concave notch at base (1)
5.	SECONDARY VENATION: brochidodromous (0), eucamptodromous (1), craspedodromous (2), bohlenioid (along side, alternate veins enter teeth, others approach sinuses and bifurcate; Wolfe and Tanai, 1987; Wolfe and Weher, 1987) (3), billioid (closely spaced, 45-75° from midrib, arching upward within margin and trailing close to it, giving off numerous external tertiary branches to the margin, commonly accompanied by inter-secondary veins set at right angles to midrib) (4) (ordered: 0>1>2>3; 1>4)
6.	STIPULES: absent (0), present (1)
7.	SEPALS: distinct (0), connate (1)
8.	PETALS: flat, ovate to elliptic (0), with two inflexed auricle-like basal lobes (1), with scale across adaxial surface (2), with a prolonged basal hornlike, digitate, or hooded appendage (3), with two long, fleshy, marginal horns (4), with two raised marginal ridges (5) (ordered: 0>1>3>2; 1>4>5)
9.	PETALS: clawed (0), without a claw (1)
10.	NECTAR DISK: intrastaminal (0), extrastaminal (1)
11.	NECTAR DISK: not invaginated at petal insertion (0), invaginated (1)
12.	DISK/STAMEN INSERTION: disk with stamen insertion concentric with axis (thus, flowers usually actinomorphic) (0), stamen insertion eccentric (flowers zygomorphic) (1)
13.	STAMENS: glabrous (0), pilose (1), papillose (2) (ordered)
14.	STAMEN NUMBER: 10 (or 15) (0), 8 (1), 7 or fewer (2) (ordered)
15.	ANTHER APPENDAGES: absent (0), apical (1), apical and basal (2)
16.	POLLEN SHAPE: spherical to round-prolate (0), triangular-oblate (1)
17.	CARPEL NUMBER: 5 (0), 3 (1), 2 (2) (ordered)
18.	STYLES: branched (0), unbranched (1)
19.	OVARY: sessile (0), stipitate (may be expressed only in pistillode) (1)
20.	PLACENTATION: medial to apical (0), basal (1)
21.	FUNICULUS: present, ovule not appressed to obturator (outgrowth of ovary wall) (0), absent, ovule appressed to obturator (1)
22.	OVULE NUMBER: 2 or more per carpel (0), 1 per carpel (1)
23.	OVULE(S): erect (0), hippocastanoid (obturator elongate, geniculate, ovules of the pair back-to-back, half twisted about one another; van der Pijl, 1957) (1)
24.	FRUIT: not inflated (0), inflated along dorsal walls of locules (1), winged by adpression of inflated dorsal walls of locules (2)
25.	FRUIT: capsular (0), schizocarpic (1), pseudomonomerous, leathery, berry-like (2)
26.	PERICARP: homogeneous (0), with sclerotic inclusions (1)
27.	EMBRYO straight (micropyle adjacent to hilum), seed without radicular pocket (0), bent (micropyle adjacent to hilum), seed with radicular pocket (radicle separated from rest of embryo by deep fold in seed coat); or embryo straight (micropyle opposite hilum), seed without pocket (1)

and forming an apparently single vein complex proximally; and anthers dorsi- vs. basifixed) may be useful in studies within smaller, more completely sampled groups. In particular, the presence of an arilloid sarcotesta (van der Pijl, 1957; see also Corner, 1976) may be plesiomorphic in the Sapindaceae, being a synapomorphy for the Sapindaceae plus Meliaceae. The various modifications of this sarcotesta may be phylogenetically informative; its loss, however, appears to be correlated with the evolution of indehiscent fruits and shows considerable parallelism.

Results. The PAUP analysis yielded 16 trees of 82 steps with a CI of 0.50 (0.49 when uninformative characters are disregarded; RI= 0.68). Common to all trees are four well supported clades (Figs. 7-9). The first is the hippocastanoid clade, which comprises the two genera of Hippocastanceae (*Aesculus* and *Billia*) along with the sapindaceous *Handeliodendron*. These genera are united by their oppo-

TABLE 18. Sapindaceae/Aceraceae/Hippocastanaceae Matrix (*=characters with notes; ?=missing; a={0/1})

		*				
	**	* 1		2	* *	*
	12345	67890	12345	67890	12345	67
Rutales	0000a	000a0	00a00	00a00	0000?	00
Aesculus	11014	01401	01122	01110	10100	11
Billia	11014	00401	01022	01110	10100	11
Handeliodendron	11014	00501	01121	01110	10100	11
Hypelate	00000	00011	00011	01100	10002	01
Koelreuteria	000?2	00101	00110	01100	10010	01
Delevaya	00002	00301	00011	02100	00010	01
Ungnadia	00002	01301	11010	01110	10010	01
Talisia	001?0	00111	10111	a1101	11002	01
Sapindus	00101	00101	10110	01101	11001	01
Cupania	001?2	00101	10110	01001	11000	01
Euphoria	00101	01011	10110	02001	11001	01
Thouinia	000?2	00201	11110	11001	11021	01
Athayana	00003	01301	11110	01101	11021	01
Bridgesia	02003	00211	11111	01000	11021	01
Diatenopteryx	00002	00311	1a111	02000	11021	01
Thinouia	00002	10201	10111	01001	11021	01
Serjania	00003	10301	11110	11000	11021	01
Acer	12013	00011	1021?	02000	10021	01
Dipteronia	10013	00001	10211	02000	10021	01

4: In *Koelreuteria*, *Talisia*, and *Cupania* the condition is more or less intermediate or not clearly discernable. **5:** *Koelreuteria* is variable, with semicraspidodromous venation as well as state 3 (but not clearly equivalent to 3 in other taxa); state 2 is considered ancestral in the genus. **8:** *Aesculus* is polymorphic for 4 and 5; state 4 is considered ancestral in the genus because the presence of this particular kind of petal appendage is considered ancestral to the presence of a reduced/vestigal appendage, as represented by two raised marginal lines. **10:** We interpret *Acer* as having stamens apical on the disk, but with the disk flattened into a very short broad cylinder, with the stamens displaced away from the ovary on the margin of the disk apex; hence, the disk is superficially "intrastaminal" (see text). **21:** van der Pijl (1957) described *Harpullia arborea* as "provided with a funicle," in contrast to the other Sapindaceae he described. It is unclear whether the funiculus in *Harpullia* is similar to those found in the outgroups, or whether it is a modified obturator. The condition in *Delevaya* is identical to that in van der Pijl's illustration and in specimens of *Harpullia*. **25:** Capsules occur in all outgroup families; drupes occur in three families, berries in the Rutaceae, and schizocarps occur in some Simaroubaceae. **27:** Seeds with a straight embryo in which the micropyle is opposite the hilum are found (among taxa included in our analysis) only in *Euphoria*; if this is coded as a separate state, the feature would be autapomoporphic for this genus (although it also occurs in the closely related, but non-analyzed, genera *Litchi* and *Nephelium*) and derived from state 1. The position of the micropyle in *Euphoria* also suggests derivation from seeds with a radicular pocket (see van der Pijl, 1957).

site and palmately compound leaves (chars. 1, 2), petiole with a basal concave notch (char. 4), billioid venation (char. 5-4), petals with two marginal appendages (char. 8-4), seven stamens (char. 14-2) positioned eccentrically on the nectar disk (char. 12), stipate ovaries (char. 19), hippocastanoid ovules (char. 23), and pericarp with sclerotic inclusions (char. 26) (Fig. 7). The second clade, including only *Acer* and *Dipteronia*, comprises the traditional Aceraceae. These two genera are united by these characters: opposite leaves (char. 1), petioles with a basal concave notch (char. 4), nonauricled petals (char. 8-0), papillose stamens centric on disk (chars. 13-2, 12-0), and two ovules per carpel (char. 22-0). The third is the samaroid clade which includes both the Aceraceae and members of the sapindaceous tribes Thounineae

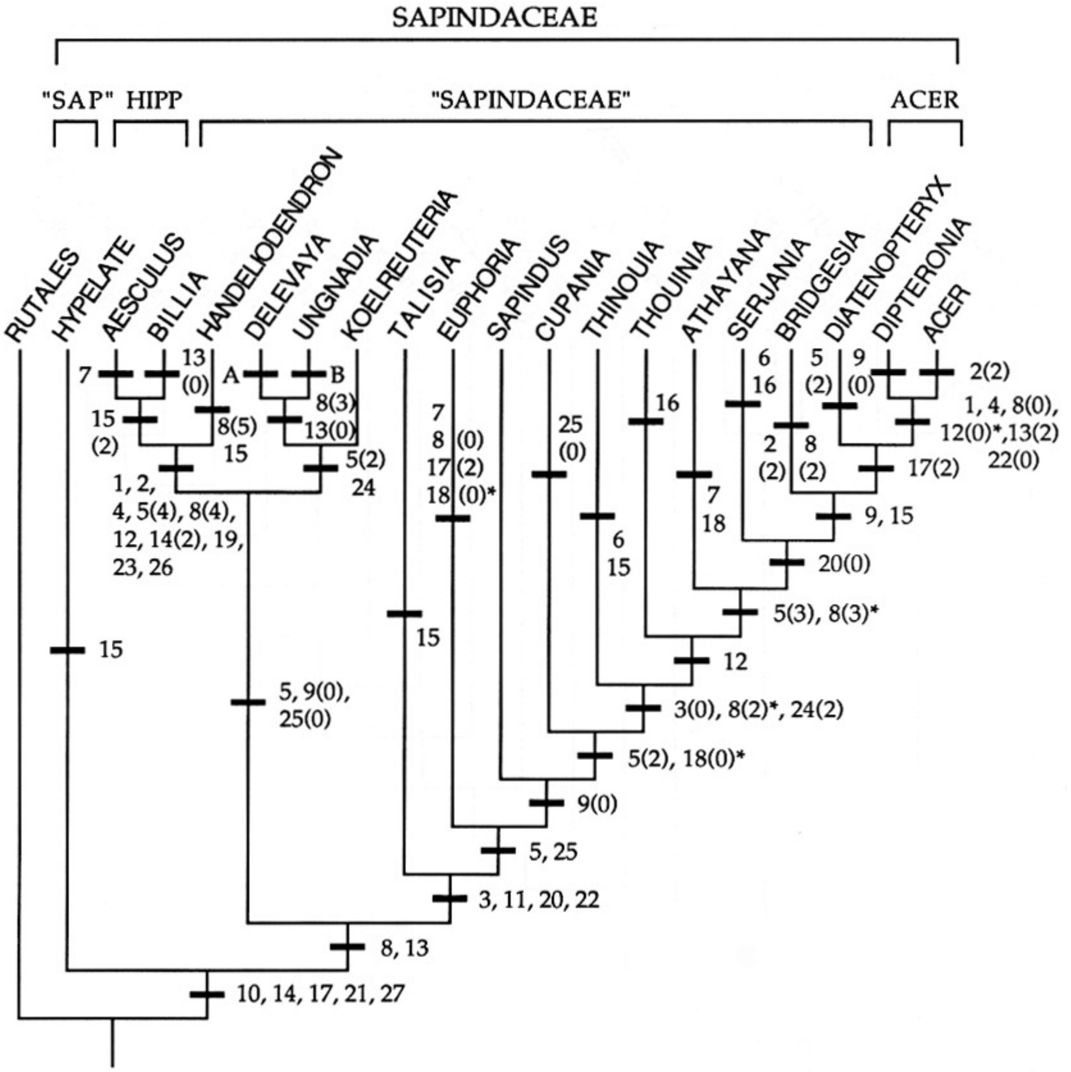

Fig. 7. Representative cladogram (82 steps) with *Koelreuteria*, *Ungnadia*, and *Delevaya* linking with Hippocastanoid clade) resulting from analysis of Sapindaceae/Aceraceae/Hippocastanaceae; CI = 0.50. * = one or more alternative placements are equally parsimonious; A = 15, 19(2), 21(0); B = 7, 11, 12, 19.

and Paulinieae: *Thouinia, Thinouia, Athayana, Serjania, Bridgesia*, and *Diatenopterys*. These genera share the reversal to branched styles (char. 18) and distinctive, winged (char. 24-2), schizocarpic fruits.

The final or sapindoid clade is composed of the samaroid clade plus those additional genera that further represent subfamily Sapindoideae: *Cupania*, *Euphoria*, *Sapindus*, and *Talisia.* These genera are united on the basis of invaginated petal insertions (char. 11), basal placentation (char. 20), and reduction to one ovule per carpel (char. 22).

In all of the most parsimonious trees *Koelreuteria*, *Delevaya*, and *Ungnadia* formed a distinct clade on the basis of craspedodromous venation (char. 5-2) and inflated fruits (char. 24). Some of the trees (Fig. 7) had this clade united with the hippocastanoid clade by clawed petals and capsular fruits (two homoplasious

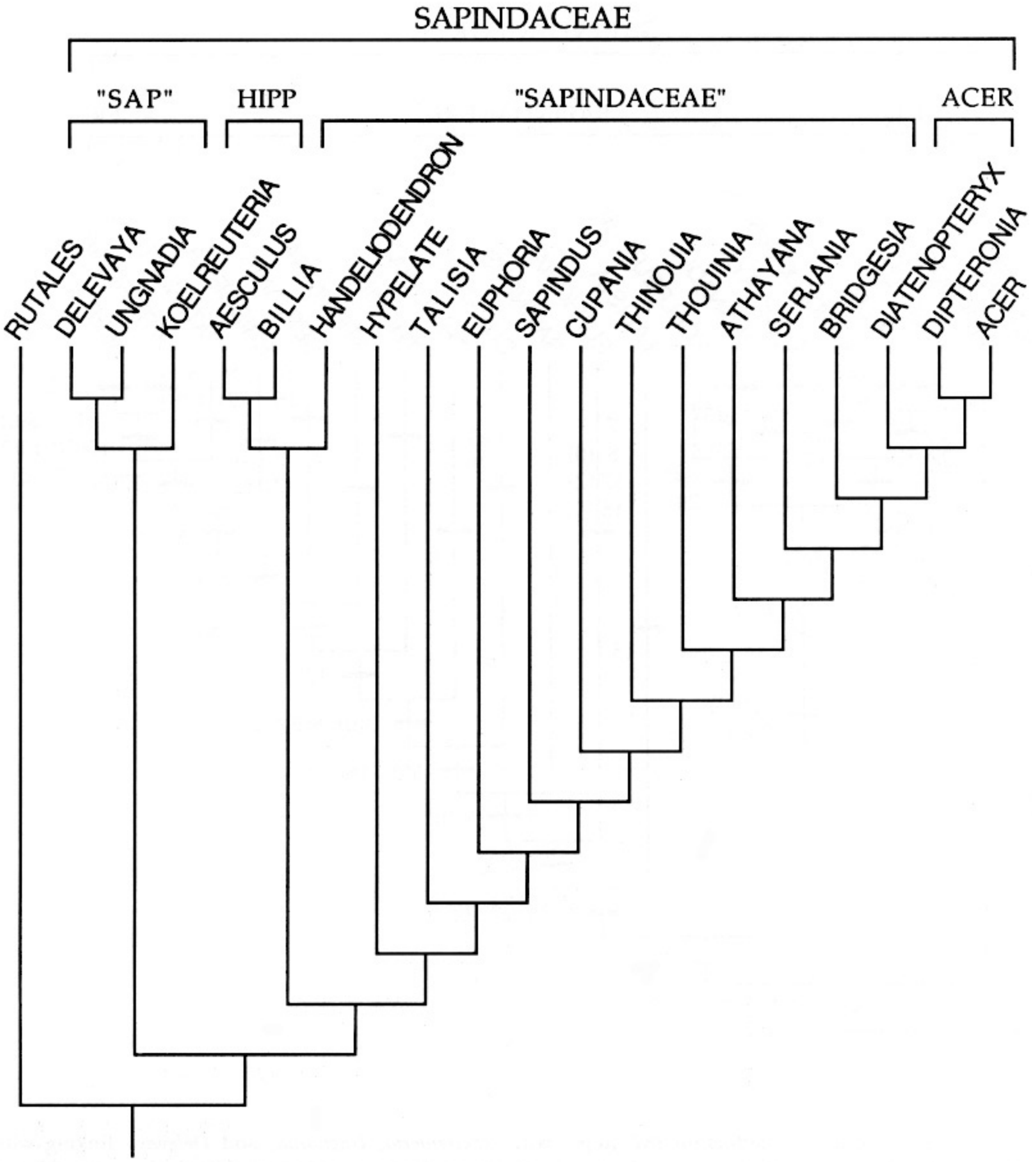

Fig. 8. Representative cladogram (with *Koelreuteria*, *Ungnadia*, and *Delevaya* forming part of a basal dichotomy) resulting from analysis of Sapindaceae/Aceraceae/Hippocastanaceae; CI = 0.50.

features) while in others this group was a "basal" branch (Fig. 8).

An analysis with all of the multistate characters unordered yielded two trees of 78 steps (CI=0.51 excluding uninformative characters; RI=0.69), which are quite similar to those outlined above. The same four major clades are evident, the Hippocastanaceae and Aceraceae are nested within Sapindaceae, and *Hypelate* is the sister-group to the remaining genera in the analysis. The one significant difference is that *Ungnadia*, *Delevaya* and *Koelreuteria* were a paraphyletic group within which the hippocastanoid clade was nested.

Discussion. Sapindaceae as currently delimited in various evolutionary classifications (Radlkofer, 1896; Tahktajan, 1980; Dahlgren, 1980, 1983; Cronquist, 1981; Thorne, 1976,

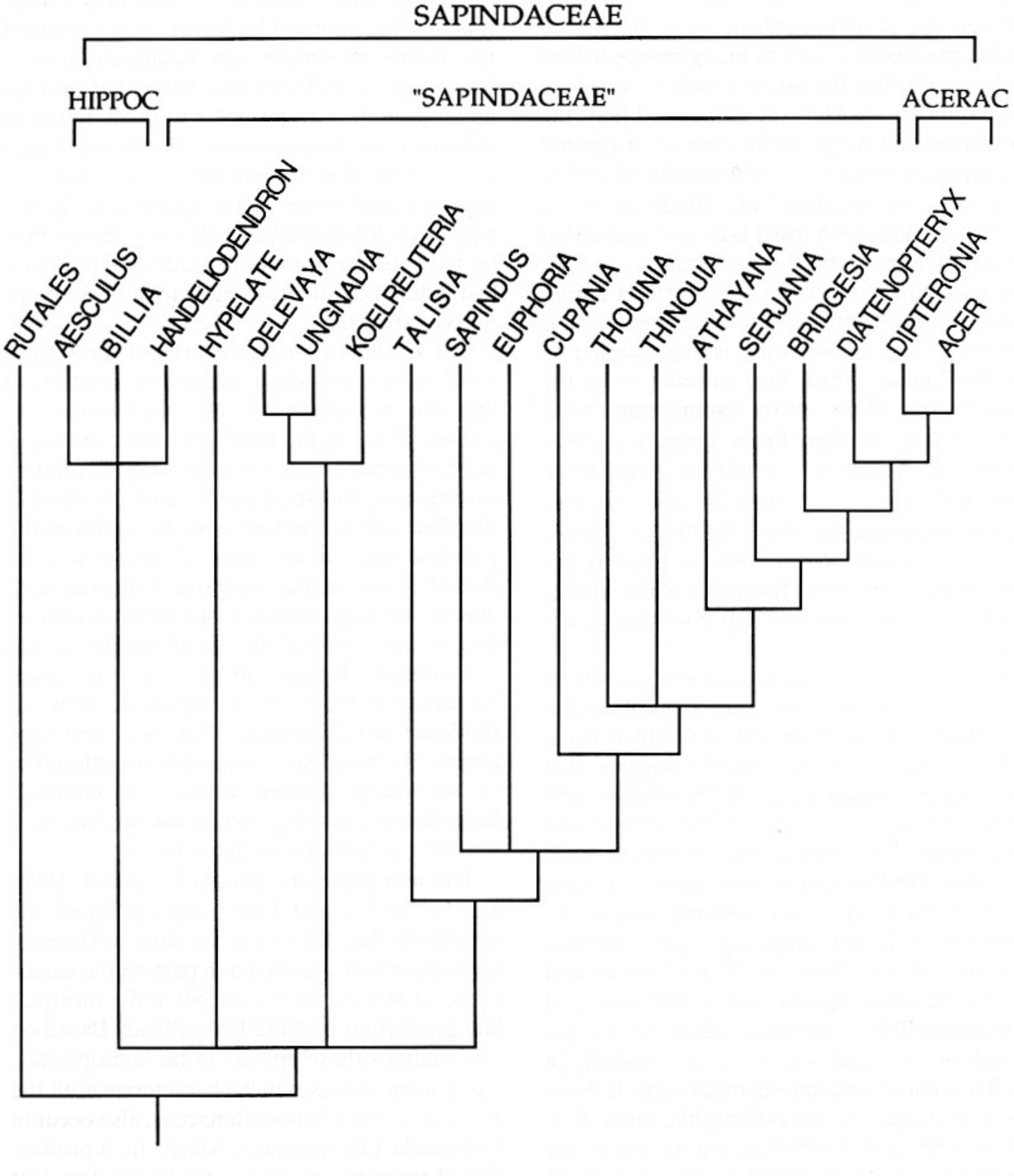

Fig. 9. Strict consensus of 16 trees resulting from analysis of Sapindaceae/Aceraceae/Hippocastanaceae.

1983) are clearly paraphyletic. Aceraceae and Hippocastanaceae are probably monophyletic (see Fig. 9). The published tribal classifications of the Sapindaceae (Radlkofer, 1896; Melchior, 1964; Muller & Leenhouts, 1976) need further revision because of the large number of potentially polyphyletic or paraphyletic groups, as is illustrated by the current placement of genera included in our analyses (Fig. 7).

Three competing hypotheses concerning the relationships of Aceraceae and Hippocastanaceae have been published either explicitly or implicitly. (1) Radlkofer (1890, 1896) considered both of these temperate families related to subfamily Dodonaeoideae tribe Harpullieae, which he considered derived within Sapindaceae. (2) Muller and Leenhouts (1976) studied pollen characters and agreed with the relationship to the Harpullieae, but they explicitly showed the Dodonaeoideae (plus Aceraceae and Hippocastanaceae) as being monophyletic and constituting the sister group to much of the Sapindaceae. They (p. 407) stated that "the Aceraceae and Hippocastanaceae are suggested to represent tribes near the Harpullieae, rather than separate families." (3) Wolfe & Tanai (1987), working with fossil taxa, concluded that the extant Sapindaceae and Aceraceae evolved from a common ancestor in an extinct Sapindaceous tribe represented by the fossil genus *Bohlenia.* This extinct tribe is most similar to the Paullinieae, which they consider to be the basal lineage of the extant Sapindaceae. They concluded (p. 8) that "From a purely cladistic viewpoint, Aceraceae should be given tribal rank in Sapindaceae." They did not comment on the Hippocastanaceae. Radlkofer considered the Paullinieae primitive (i.e., having numerous plesiomorphic features), while Muller and Leenhouts suggested that it was highly derived.

In a general way, our results support a relationship of the Aceraceae and the Thouinieae/Paullinieae, as proposed by Wolfe & Tanai (1987). Specifically, our results suggest that *Diatenapteryx*, *Bridgesia*, (both Thouinieae) and *Serjania* (Paullinieae) are the first, second, and third outgroups, respectively. However, their view that the Paullinieae and Aceraceae have retained many ancestral features within the Sapindaceae is not supported. They reached this view, in part, because the Paullinieae and Aceraceae have multiseriate wood rays and nonseptate fibers, characters which we did not include in our analyses owing to variability in the Thouinieae and among outgroups. If these wood features are plesiomorphic, then it is conceivable that synapomorphic reversals (or parallel reversals) occurred in these advanced taxa.

Wolfe and Tanai (1987) placed considerable importance on the fossil genus *Bohlenia,* which is known only from dispersed leaves and fruits. The leaves are pinnately compound, ternately organized, lobed and toothed, with bohlenioid venation (see Wolfe & Wehr, 1987); they closely match the leaves of many Paullinieae. However, although the leaves of Aceraceae have bohlenioid venation, they are more similar to leaves in the Thouinieae. For example, both *Acer* and *Bridgesia* (Thouinieae) have retained the toothed lobing but have reduced the leaves to simple and palmately veined. *Dipteronia* lacks lobes and has strictly evenly imparipinnate leaves similar to those found in *Athayana* and *Diatenopteryx.* Wolfe and Tanai (1987) note that bohlenioid venation also occurs in *Dilodendron* of the Cupanieae. If this type of venation evolved only once, then it may be basic to the sapindoid clade, having been lost independently from most members except the samaroids.

The fruits of *Bohlenia* consist of three samaroid mericarps, which are nearly identical to the two mericarps of the aceraceous *Dipteronia*. That is, the locule of each mericarp is centrally placed with a circular wing completely surrounding the seed cavity, and the seed is supplied with a vein that runs the radius of the proximal side of the wing. *Bohlenia* was included in our initial analyses. Unfortunately, due to the large number of unknown characters, it was topologically labile within the samaroid clade. If, however, the waferlike, circular samaroid mericarp is a synapomorphy for *Bohlenia* and *Dipteronia*, then *Acer* and *Dipteronia* are most parsimoniously considered to be separately derived within the samaroid Sapindaceae, making Aceraceae diphyletic if *Bohlenia* is retained in Sapindaceae.

The acceptance by Radlkofer (1890, 1896) and by Muller and Leenhouts (1976) of the hypothesis that Aceraceae are close to Harpullieae apparently was based in part on the occurrence of two ovules per carpel and a bicarpellate gynoecium in some Harpullieae. Based on our analyses these appear to be homoplastic.

Opposite leaves, which characterize both the Aceraceae and Hippocastanaceae, also occur in *Valenzuela* (Thouinieae), which, in reproductive characters, resembles *Bridgesia.* The leaf blades are small, sessile, entire-margined, plynerved, and with reduced venation. *Valenzuela* was included in our initial analyses, but because its position in the samaroid clade was so labile, it was deleted from later analyses. In all cases, however, its opposite leaves were interpreted as parallelisms with the Aceraceae, and therefore, it is considered of limited importance in elucidating the genealogical relationships of Aceraceae. In several features the Aceraceae appear to be distant from the Thouinieae/Paullinieae. For example, the disk in many members of *Acer* has been described as being intrastaminal (Wolfe & Tanai, 1987), as in the outgroups. Instead, we interpret *Acer* as having stamens apical on the disk (as in *Koelreuteria*, with an extrastaminal disk), but with the disk flattened to a very short broad cylinder so that the stamens are displaced peripherally away from the ovary on the margin of the disk apex. Likewise, the regular flowers of *Acer* have elliptic, unclawed petals without auricles or appendages. We suggest that the claw is developmentally supressed (as in *Diatenopteryx* and *Bridgesia*), and the associated appendage subsequently lost.

The hypothesis that Hippocastanaceae are related to the Harpullieae via *Delevaya*, *Handeliodendron*, and *Ungnadia* (Radlkofer, 1890, 1896; Muller & Leenhouts, 1976) is only supported in part by our results. First, the placement of *Handeliodendron* in the Harpullieae appears to stem from Rehder's (1935) reluctance to enlarge the tightly circumscribed Hippocastanaceae at the expense of the already heterogenous Sapindaceae (in accordance with traditional taxonomic practice, later codified as "McVaugh's rule," McVaugh, 1943).

Even from the standpoint of traditional taxonomic methods, *Handeliodendron* should probably have been placed in the same suprageneric taxon with members of the Hippocastanaceae. In some of our cladograms, it even appeared to be derived within the hippocastanoid clade, sharing the synapomorphy of pilose stamens with *Aesculus*. Among the 16 cladograms, the hippocastanoid clade was positioned either near the base of the Sapindaceae as an independent line or as the sister-group of the *Koelreuteria-Delevaya-Ungnadia* clade (Koelreuterieae plus Harpullieae).

In conclusion, Aceraceae and Hippocastanaceae are substantiated as being derived within Sapindaceae. Because the Sapindaceae are paraphyletic, the family circumscription should be expanded to include the common ancestor of plants now assigned to Sapindaceae, Aceraceae, and Hippocastanaceae, and all of its descendants. This circumscription is in partial agreement with the broad family circumscription of Bentham and Hooker (1862), and with Thorne's (1992b) recent treatment. It is of interest that Hutchinson (1926) also included Hippocastanaceae within Sapindaceae. Synapomorphies for the Sapindaceae, as circumscribed here, include the extrastaminal nectar disk (char. 10), eight or fewer stamens (char. 14), three (or only two) carpels (char. 17), ovules associated with an obturator (char. 21) that leaves a prominent scar on the seed, and seeds with a bent embryo and a radicular pocket (char. 27). Most Sapindaceae have petal appendages (char. 8) and pilose stamens (char. 13) (see Tables 17, 18), and it is very likely that these features evolved early in the evolution of Sapindaceae (Fig. 7, 8). The most likely explanation for the absence of the latter in a few sapindaceous genera is that reversals have occurred; however, the lack of petal appendages and pilose stamens in *Hypelate* may be ancestral (Fig. 7). In addition, Sapindaceae are distinctive in their possession of a great variety of cyclopropane amino acids (Umadevi & Daniel, 1991). As discussed by Heimsch (1942) the wood anatomy of this group is also distinctive, e.g., all have homogeneous rays. Further work is needed to delimit monophyletic groups within the Sapindaceae, but the genus *Handeliodendron* should be transferred from the Harpullieae to the infrafamilial taxon containing *Aesculus* and *Billia*.

SIMILAR PATTERNS IN OTHER GROUPS

In addition to the six groups analyzed above, we have conducted a survey of other clusters of closely related angiosperm families. Those for which there are preliminary phylogenetic data are briefly discussed below. Most of these family pairs show a phylogenetic pattern similar to that seen in our six primary examples. Saururaceae/Piperaceae, however, may be an example in which both families are monophyletic. No examples have been found in which the predominantly temperate family is paraphyletic.

Bombacaceae/Malvaceae. These two groups are likely united by the synapomorphy of a more or less monadelphous androecium of numerous half-anthers. They share several apomorphies with Tiliaceae and Sterculiaceae, especially the presence of mucilage canals and stellate hairs, and together these comprise the "core" Malvales; preliminary analyses based on *rbc*L sequence data also support the monophyly of the "core" Malvales (Chase et al.

1993). The Bombacaceae are very diverse, woody and tropical, and likely paraphyletic (having no potentially synapomorphic similarities that are not also shared with Malvaceae), while the Malvaceae are woody to herbaceous, and widely distributed (with many temperate herbaceous species). Taxa of Malvaceae seem to be united only by the synapomorphy of spiny pollen (a character traditionally used to separate this group from the Bombacaceae). Two specialized tribes of Malvaceae (Malveae and Ureneae) have the additional derived character of a schizocarpic fruit, while the Hibisceae retain the presumed primitive fruit condition of the Malvales, a loculicidal capsule. The Hibisceae have sometimes been placed in Bombacaceae, with fruit type instead of pollen exine being stressed in family delimitation (see Edlin, 1935).

The Bombacaceae and Malvaceae probably should be united into a single family. Problems also occur in family delimitation in relation to Tiliaceae and Sterculiaceae (Manchester, 1992). A phylogenetic analysis of the "core" Malvales is needed, and it is possible that all four families will have to be united. This would be a practical benefit, as members of these "families" cannot be distinguished in vegetative condition. Brown (1818) noted that the families of the Malvales were roughly equivalent to the tribes of the Rosaceae.

Fabales. Three subgroups are generally recognized within Fabales; in most classifications these are considered subfamilies (Caesalpinioideae, Mimosoideae, Papilionoideae [Faboideae]; Polhill and Raven, 1981) of Fabaceae (Leguminosae), but they are sometimes treated as separate families (Cronquist, 1981). Nevertheless, it is widely believed that Caesalpinioideae are paraphyletic, with some genera more closely related to Mimosoideae and some more closely related to Papilionoideae than they are to one another (Polhill, 1981). This view appears to be corroborated by preliminary phylogenetic analyses of morphological characters, although the results are sensitive to the choice of outgroups (J. Chappill, pers. comm.). Within Papilionoideae it is clear that temperate herbaceous lines are more recent derivatives of tropical woody groups, yet the number of originations remains uncertain. Based on loss of the chloroplast DNA inverted repeat (Lavin et al., 1990) it appears that five northern temperate, predominantly herbaceous, tribes (Galegeae, ca 2540 species; Hedysareae, 263; Vicieae, 298; Cicereae, 40; Trifolieae, 477) are united with Carmichaelieae (ca 7 species of woody plants of New Zealand) and with *Wisteria* (ca 6 sp. of eastern Asia and eastern North America). The latter are woody plants presumably derived from tropical ancestors with the inverted repeat (other Millettieae; Lavin et al., 1990), although there are indications that some other Millettieae may also lack the inverted repeat (Liston, 1992). Under this view, two other tribes of temperate herbs - Loteae and Coronilleae - must have originated independently, possibly from within Phaseoleae (Lavin et al., 1990). Although these two major groups of temperate tribes differ in a number of ways (seedling morphology, pollen morphology, chromosome number), separate origins of temperate herbaceous lines would entail the independent evolution of a number of morphological characters (closed vascular system, adnate stipules), which have sometimes been cited as evidence of a close relationship (e.g., recognition of the "epulvinate series" within the galegioid complex; Polhill, 1981).

The alternative hypothesis is that Loteae and Coronilleae are closely related to the five tribes that lack the inverted repeat, in which case most of the temperate herbaceous Papilionoideae form a clade. This would imply that the inverted repeat was lost more than once. Indeed, if Carmichaelieae are related to Liparieae (of South Africa) and Bossiaeeae (of Australia), and if *Wisteria* is related to some Phaseoleae, as suggested by J. Chappill (pers. comm.), there would have been at least three losses of the inverted repeat.

Although the phylogenetic relationships of the temperate, herbaceous groups of Papilionoideae are still not well resolved, it seems clear that separation of these groups has resulted in one or more paraphyletic tribes of tropical, woody plants.

Clusiaceae/Hypericaceae. A cladistic analysis of the Clusiaceae (Stevens, 1988) indicates that the family is paraphyletic if Hypericaceae (with many shrubby to herbaceous temperate species) are segregated. Other workers have reached the same conclusion by using phenetic or evolutionary taxonomic criteria; see Wood

& Adams (1976), Thorne (1983), and Robson (1977).

Ehretiaceae/Boraginaceae. Among modern evolutionary taxonomists, only Dahlgren (1975, 1980, 1983) recognized two families for the gynoterminal and gynobasic members of this group (Al-Shehbaz, 1991). Cantino (1982), Olmstead et al. (1992), and Downie and Palmer (1992) demonstrated that this group is not the sister group of Verbenaceae/Lamiaceae. Therefore, the characteristic gynoecium in these groups has evolved convergently. This suggests that the tropical Ehretiaceae, with a terminal style, are a paraphyletic complex. Johnston (1950, p. 176) stated that "there are many reasons for believing that the original Boraginaceae were ehretioid in character and that from them have evolved in divergent lines of specialization the three other subfamilies, the Cordioideae, Heliotropioideae, and Boraginoideae."

Flacourtiaceae/Salicaceae. *Populus* and *Salix* (Salicaceae) are likely cladistic relatives of *Idesia* (Idesideae) and other genera of the extremely heterogeneous (and presumably paraphyletic) Flacourtiaceae. Salicaceae and *Idesia* are linked by the derived characters of salicoid teeth (see Hickey & Wolf, 1975) and the presence of salicin (Cronquist, 1988). The Salicaceae and Idesideae also share actinodromous venation. Thorne (1981, p. 244) stated that "The Salicaceae, despite the basic anemophily of *Populus* L. and secondary entomophily of *Salix* L., approach the Flacourtiaceae, especially the temperate Asiatic *Idesia polycarpa* Maxim." He also noted that "Meeuse (1975) found a positive association between the Salicaceae and Flacourtiaceae in respect to both embryological and chemical characteristics." Floral reduction has occured in some members of the Flacourtiaceae, and genera such as *Banara* are likely basal members of the salicoid-idesioid clade.

Myrsinaceae/Primulaceae. A detailed phylogenetic study of the Primulales is needed. We suspect that the woody and tropical Myrsinaceae are a paraphyletic group that has given rise to the mainly temperate and herbaceous Primulaceae. It is noteworthy that *Lysimachia* (Primulaceae) possesses scattered schizogenous secretory ducts or cavities (appearing as black to reddish lines or dots) as do the Myrsinaceae. Theophrastaceae likely are monophyletic (Ståhl, 1990).

Papaveraceae/Fumariaceae. The Papaveraceae are clearly paraphyletic, with Fumariaceae nested within their cladistic structure. Assuming a *Ranunculus*-like plant as the outgroup (see Thorne, 1974; Chase et al., 1993), the Papaveraceae (defined broadly) show the synapomorphies of a syncarpous gynoecium, parietal placentation, capsular fruits, caducous calyx, arillate seeds, and presence of laticifers (colored sap). In addition, most have wrinkled petals. The most primitive genera probably are in the tribe Platystemoneae; *Platystemon* shows only slightly fused carpels (with free stigmas) that separate from each other at maturity. Other members of the Papaveraceae/Fumariaceae clade, e.g., *Papaver* and *Argemone*, have completely fused carpels.

More specialized groups, e.g., *Chelidonium* and *Sanguinaria*, show a reduction to only two carpels, and have elongate fruits with a replum-like structure and two valves separating at maturity – a fruit type convergent with that of the Brassicaceae. The Chelidonieae likely include the clade comprising Fumariaceae s.l., characterized by having flowers in which the two outer petals look slightly different from the two inner petals, six (or fewer) stamens, and a loss of latex (although they have tissues with elongate idioblasts, probably reduced laticifers, and watery sap). *Hypecoum* and *Pteridophyllum* show these characters, and likely are early branches within Fumariaceae s.l. The more derived members of the Fumariaceae (Fumariaceae s.s.) share several additional characters: one or two saccate or spurred petals (associated with a nectar gland) and thus flowers in which the two outer petals look extremely different from the two inner petals; two inner petals connate or connivent over the stigma; and stamens fused into two groups of three (diadelphous), in which the central stamen (of each group) has four locules (ancestral condition) and the two lateral stamens (of each group) have only two locules. Genera showing these additional synapomorphies include *Dicentra*, *Corydalis*, and *Fumaria*. *Fumaria* (in Fumarieae, the remaining genera are in Corydaleae) shows additional apomorphies: reduced ovary with a single ovule, and nut-like indehiscent fruits (associated with loss of the replum-like structure).

Fumaria, *Dicentra*, and *Corydalis* are usually recognized (at least by many American systematists) as a distinct family, Fumariaceae (see Cronquist, 1981). The intermediate genera *Hypecoum* and *Pteridophyllum* are sometimes placed in Fumariaceae, sometimes placed in Papaveraceae, sometimes placed in the segregate family Hypecoaceae, and sometimes placed each in its own family - Hypecoaceae and Pteridophyllaceae (see discussion in Cronquist, 1981). The close relationship between Fumariaceae s.s., *Hypecoum* and *Pteridophyllum*, and *Chelidonium* and *Sanguinaria* (which together form a monophyletic group), is supported by Dahl (1990) and Lidén (1986).

The separation of Fumariaceae (as well as smaller segregates like Hypecoaceae; see Dahlgren, 1980, 1983) render Papaveraceae paraphyletic, and we recommend that the group be treated as a single family - Papaveraceae (as in Melchior, 1964; Thorne, 1974, 1983, 1992a, 1992b; Takhtajan, 1980; Lidén, 1986), not as two to several families (as in Dahlgren, 1980, 1983; Cronquist, 1981; Lawrence, 1951; Ernst, 1962).

We agree with Thorne (1974, p. 190) who united the families on the grounds that to accept the Fumarioideae as "a distinct family one would have to ignore the basic papaveraceous habit, foliage, stem anatomy, chemistry, cytology, and fruits of the fumitories and the two listed intermediate genera with their mildly bilaterally symmetrical corollas and four free stamens." Recent analyses based on *rbc*L sequence data also support the paraphyly of the Papaveraceae (see Chase et al., 1993).

Saururaceae/Piperaceae. It is noteworthy that the detailed cladistic analyses of Tucker et al. (1993) as well as the preliminary *rbc*L analyses of Chase et al. (1993) indicated that Saururaceae, an herbaceous and more or less warm temperate family, likely are monophyletic, and are the sister group of the tropical and frequently woody Piperaceae. Tucker et al. (1993, p. 634) noted that "*Saururus* represents the most primitive extant member of Piperales, and the other saururaceous taxa and piperaceous taxa represent separate evolutionary lineages within Piperales" from a *Saururus*-like ancestor. The herbaceous condition likely is ancestral. Woodiness is probably derived in Piperaceae with a reversal to the herbaceous condition in *Peperomia* (Tucker et al., 1993).

Verbenaceae/Lamiaceae. The Lamiaceae (Labiatae), a diverse group in temperate regions, generally has been accepted as monophyletic, though closely related to the more tropical Verbenaceae. It is distinguished from the latter only by the gynobasic style. Two precladistic studies, however, provided evidence suggesting that the Lamiaceae might, in fact, be polyphyletic. Junell (1934) studied gynoecial morphology and found that the labiate tribes Ajugeae and Prostanthereae are more similar to the verbenaceous Viticoideae and Chloanthoideae, respectively, than to the remaining Labiatae. In a phenetic morphological analysis, El-Gazzar and Watson (1970) obtained at least two phenetic groups in which lamiaceous and verbenaceous genera clustered together, separated from the remaining genera of the two families.

A continuing series of phylogenetic studies of morphology, palynology, anatomy, and chemistry by Cantino and his associates (Abu-Asab, 1990; Abu-Asab & Cantino, 1989; Cantino 1982, 1990, 1992a; Cantino & Sanders, 1986; Chadwell et al., 1992) has been directed at understanding the relationships of the Lamiaceae. These have provided strong support for the polyphyly of Lamiaceae. That is, the partially gynobasic style evolved several times in parallel and other characters are more reliable indicators of phylogenetic relationships.

Cantino's (1992a, 1992b) recent analysis is the most definitive work to date. Based on a data matrix of 106 genera and subgeneric taxa scored for 85 characters, he investigated the possible sister-group relationships of all labiate lineages. Cantino's selection of verbenaceous taxa was based on Junell's (1934) discovery that all the labiates he examined shared with the majority of Verbenaceae the character of having the ovules attached to the sides of the false partitions of the ovary rather than on the margins, as in the Verbenoideae. Although Cantino (1982) had previously established the Bignoniales as an appropriate outgroup for Lamiales, it was impractical to survey all characters in all members of the Bignoniales in addition to carefully evaluating the ingroup taxa. Therefore, he employed the Verbenaceae with marginal ovules as outgroups to root the resulting networks by the Lundberg method. Although a precise rooting position was not found the convergent evolution of partial gynobasic styles was confirmed. Perhaps more surprising was his conclusion that the Lamiaceae were derived within Verbenaceae in no fewer than four separate clades.

The sister-group relationships were as follows: 1) all fully gynobasic-styled labiates plus four "primitive" genera of Ajugeae formed a clade with *Garrettia* (Viticoideae), 2) the labiate Scutellarieae plus two genera of Ajugeae formed a clade with *Holmskioldia* (Viticoideae), 3) the group of labiate Prostanthereae either formed a basal branch or was linked with the Chloanthoideae, 4) *Trichostema*, *Schnabelia*, *Rubiteucris*, and *Amethystea* (Ajugeae) plus the next clade (# 5), formed a clade with *Karomia* (Viticoideae) and certain species of *Caryopteris* (Caryopteridoideae) and *Clerodendrum* (Viticoideae), and 5) *Teucrium* (Ajugeae) formed a clade with *Spartothamnella* (Chloanthoideae), and *Teucridium* and *Oncinocalyx* (Viticoideae); see Cantino (1992a, 1992b) for a more detailed discussion of relationships and for synapomorphies supporting the five clades outlined above.

In order to maintain the Verbenaceae and Lamiaceae as two monophyletic families, Cantino (1992b) resurrected a proposal by Junell (1934) to redefine family limits. That is, the Verbenaceae is restricted to the Verbenoideae (excluding Monochileae) and the Lamiaceae is greatly expanded to include those Verbenaceae with lateral ovules on the false partitions and more or less cymose inflorescences (i.e., Caryopteridoideae, Chloanthoideae, Viticoideae, Monochileae, and possibly Symphorematoideae and Avicennioideae). He cited the lateral ovules as a possible synapomorphy of the Lamiaceae sensu Junell, and stated, "Ultimately, Junell's classification would be preferable to the other alternatives proposed here [viz., Lamiaceae simply submerged into the Verbenaceae, or Lamiaceae reduced and monophyletic while the Verbenaceae slightly expanded and paraphyletic], because it would rectify the paraphyly of the Verbenaceae as well as the polyphyly of the Labiatae."

The Verbenaceae, as delimited by Junell (1934) and Cantino (1992a, 1992b), is hypothesized to be monophyletic on the basis of marginally attached ovules, the thickening of the pollen exine adjacent to the apertures (Chadwell et al., 1992), conspicuous stigmatoid tissue (El-Gazzar & Watson, 1970), absence of uniseriate trichomes on the leaves (Cantino, 1990), and racemose inflorescences; the group may include *Phryma* (see discussion in Chadwell et al., 1992). A very similar approach to the group has been accepted by Thorne (1992b).

Cantino's basic conclusions, including the monophyly of the Lamiaceae and Verbenaceae, as redefined, have been supported by phylogenetic analyses based on *rbc*L sequence data (Olmstead et al., 1992, 1993; Chase et al., 1993). It is clear that the Verbenaceae are paraphyletic and that the Lamiaceae are polyphyletic, as they are delimited in modern evolutionary classifications (Cronquist, 1981; Dahlgren, 1980; Tahktajan, 1980; and Thorne, 1976, 1983).

We place Lamiaceae and Verbenaceae (as delimited by Cantino 1992a, 1992b; Cantino et al., 1992; Chadwell et al., 1992) in the Bignoniales (= Scrophulariales) because they share with the other members of this order the following apomorphies: oligosaccharides replacing starch (Dahlgren, 1975), frequent production of 6- oxygenated flavones, lack of stipules, opposite leaves, often diacytic stomates, basically zygomorphic and bilabiate (upper lip 2-lobed, lower lip 3-lobed) corollas, four stamens with the lower pair longer (Cronquist, 1981; Cantino, 1982), embryos of the onagrad type (*Veronica* variant) with conspicuous chalazal and micropylar haustoria (Yamazaki, 1974), and invagination of anther connective into the thecae (Wagenitz, 1992); see also G. Dahlgren (1989), Thorne (1992a, 1992b), and Wagenitz (1992). Within Bignoniales, we consider Lamiaceae and Verbenaceae to form a monophyletic group on the basis of the reduction to two ovules per carpel and the occurrence of false ovary partitions.

SUMMARY OF RESULTS AND RECOMMENDATIONS

The phylogenetic analyses discussed above document that Apocynaceae, Araliaceae, Capparaceae, Caprifoliaceae, Moraceae, Papaveraceae, Sapindaceae, and Verbenaceae are paraphyletic, being "defined" by the lack of the distinctive apomorphies of the related and more widespread to mainly temperate families, from which they are only arbitrarily separated. In contrast, the Asclepiadaceae, Brassicaceae, Fumariaceae, Adoxaceae, Valerianaceae, Dipsacaceae, Urticaceae, Hippocastanaceae, and Aceraceae are monophyletic, while the Apiaceae and Lamiaceae are polyphyletic.

Our cladograms (Figs. 1-9), along with those of Cantino (1992a), indicate that the more tropical families are paraphyletic, while families better developed in temperate regions are monophyletic or polyphyletic. That is, the more temperate families comprise one or more distinct clades whose sister groups are tropical genera or groups of genera. Thus, the beginnings of the more temperate family's distinctive morphological specializations are found in the related tropical family. The mainly tropical families tend to be predominantly woody, while groups better developed in the temperate zone have a higher percentage of herbaceous species. Sapindaceae, Aceraceae, and Hippocastanaceae, however, are all woody, while Papaveraceae and Fumariaceae are both mainly herbaceous.

The greater range of morphological variation seen in each of the paraphyletic "families" is a consequence of their non-comparability with the clades derived within them. When the range of variation within the derived clades is compared with that seen in their equal-aged sister group (i.e., within tropical genera or the tribal groups to which these belong) a more nearly equivalent range of morphological variation is seen. It is clear that the traditional family delimitations do not reflect phylogeny and impede progress in systematics (Donoghue and Cantino, 1988). We recommend recognition of the monophyletic families circumscribed above (see Table 19), defined by ancestry and diagnosed by the synapomorphies identified in the analyses above. In teaching, this should emphasize the morphological diversity within the tropical taxa, and highlight the specializations of temperate lineages.

It is important to remember that the families proposed herein are only equivalent by virtue of being monophyletic. The designation of family rank for a group is not nearly so important as is the determination of monophyletic groups and the recognition of monophyletic taxa. It should also be noted that although we are recommending that families be recircumscribed so as to be monophyletic, and that in most cases this involves an expanded concept, this certainly does not mean the abandonment of familiar monophyletic taxa within these families. Thus, for example, the taxon now known to most botanists as the Asclepiadaceae does appear to be a monophyletic group, and it should therefore have a name. One possibility would be to continue to refer to this clade as the Asclepiadaceae, even though it is nested within a taxon that also ends in "-aceae."

While this last approach would serve to promote stability (because Asclepiadaceae would continue to apply to the same group of plants), it also violates the standard Linnean principle that taxa of the same rank cannot be nested within one another. Ultimately, in recognition that ranks are basically arbitrary, we think it may be best to simply abandon the standard Linnean system in favor of a phylogenetic taxonomy, as suggested by de Queiroz and Gauthier (1992). However, we suspect that abandonment of the Linnean system will meet with even more resistance than abandonment of the traditional circumscriptions and names of groups. For this practical reason, we are suggesting that monophyletic groups within the families we have defined should be given new names, though this is not a task that we have undertaken here. For example, what is now known as Asclepiadaceae might be recognized as Asclepiadoideae, a subfamily within our Apocynaceae. Likewise, what is now known as Brassicaceae, might be renamed Brassicoideae, Valerianaceae might be Valerianoideae, and so on. In these cases, however, care must be taken not to inadvertently create paraphyletic infrafamiliar taxa.

The arbitrary taxonomic separation of temperate and tropical representatives of monophyletic groups has not been limited to the groups presented in some detail here. As noted above, many other family groups seem to fit this pattern, and need to be investigated in more detail. This pattern may be common at infrafamilial levels as well. In each case the possession of distinctive morphological features in the more temperate family, coupled with the fact that these families are relatively better known (Walters, 1961), has led to their segre-

TABLE 19. Outline of nomenclature for families analyzed or discussed in detail in the text.

Adoxaceae Trautvetter, Estestv. Istorija Gub. Kievsk. Ucebn. Okr. 35. 1853, nom. conserv.
- Sambucaceae Batsch ex Borckhausen, Bot. Wörterbuch 2:322. 1797. (Including *Viburnum*)

Apiaceae Lindley, Nat. Syst. Bot. ed. 2. 21. 1836, nom conserv. (Nom. alt.: **Umbelliferae** A.-L. Jussieu, Gen. Pl. 218. 1789, nom. conserv.)
- Araliaceae A.-L. Jussieu, Gen. Pl. 217. 1789, nom. conserv. Note: Araliaceae is earlier than Apiaceae; however, the second paragraph of Appendix IIB of the I.C.B.N. (Greuter, 1988, p. 94) states that "the earlier name must be retained unless...one of the competing names is listed in Art. 18.5. For any family including the type of an alternative family name, one or the other of these alternative family names is to be used."

Apocynaceae A.-L. Jussieu, Gen. Pl. 143. 1789, nom. conserv.
- Asclepiadaceae R. Brown, Asclepiadeae 12, 17. 1810, nom. conserv.

Brassicaceae Burnett, Outl. Bot. 1123. 1835, nom. conserv. (Nom. alt.: **Cruciferae** A.-L. Jussieu, Gen. Pl. 237. 1789, nom. conserv.)
- Capparaceae A.-L. Jussieu, Gen. Pl. 242. 1789, nom. conserv. Note: See Appendix IIB and Art. 18.5 of the I.C.B.N. (Greuter, 1988).

Caprifoliaceae A.-L. Jussieu, Gen. Pl. 210. 1789, nom. conserv., excluding *Viburnum* and *Sambucus.*
- Dipsacaceae A.-L. Jussieu, Gen. Pl. 194. 1789, nom. conserv.
- Valerianaceae Batsch, Tab. Affin. Regni Veg. 227. 1802, nom. conserv.
  - (The names Caprifoliaceae and Dipsacaceae are both conserved and were published at the same time; the name Caprifoliaceae is here chosen as the name for the combined family.)

Fabaceae Lindley, Nat. Syst. Bot. ed. 2. 148. 1836, nom. conserv. (Nom. Alt.: **Leguminosae** A.-L. Jussieu, Gen. Pl. 345. 1789, nom. conserv.) Note: See I.C.B.N., Appendix IIB and Art. 18.5 (Greuter, 1988).
- Caesalpiniaceae R. Brown in Flinders, Voy. Terra Austr. 2: 551. 1814, nom. conserv.
- Mimosaceae R. Brown in Flinders, Voy. Terra Austr. 2: 551. 1814, nom. conserv.

Lamiaceae Lindley, Nat. Syst. Bot. ed. 2. 275. 1836, nom. conserv. (Nom. alt.: **Labiatae** A.-L. Jussieu, Gen. Pl. 110. 1789, nom. conserv.) Including Verbenaceae p.p.; see Cantino (1992a) and Cantino et al. (1992) for circumscription.

Papaveraceae A.-L. Jussieu, Gen. Pl. 235. 1789, nom. conserv.
- Fumariaceae A.-P. de Candolle, Syst. Nat. 2: 105. 1821, nom. conserv.

Sapindaceae A.-L. Jussieu, Gen. Pl. 246. 1789, nom. conserv.
- Aceraceae A.-L. Jussieu, Gen. Pl. 250. 1789, nom. conserv.
- Hippocastanaceae A.-P. de Candolle, Prodr. 1: 597. 1824, nom. conserv.
  - (The names Sapindaceae and Aceraceae are both conserved and were published at the same time; the name Sapindaceae is used here for the combined family, following Bentham and Hooker [1862].)

Urticaceae A.-L. Jussieu, Gen. Pl. 400. 1789, nom. conserv.
- Moraceae Link, Handbuch 2: 444. 1831, nom. conserv.
- Cannabaceae Endlicher, Gen. Pl. 286. 1837, nom. conserv.
- Cecropiaceae Berg, Taxon 27: 39-44. 1978.

Verbenaceae Jaume Saint-Hilaire, Expos. Fam. Nat. 1: 245. 1805, nom. conserv.
- Restricted to Verbenoideae, as recognized within a traditionally more broadly delimited Verbenaceae; see Cantino (1992a), Chadwell et al. (1992).

gation from tropical paraphyletic complexes. This has resulted from the application of traditional taxonomic procedures for grouping and ranking, which involves the weighting of certain features.

The families discussed herein certainly do not exhaust the number of paraphyletic families. Many other families are presumably paraphyletic because certain groups within them have been removed due to their specialized features. Often this relates to evolution of the parasitic or myco-parasitic habit, as in, for example: Scrophulariaceae and Orobanchaceae; Ericaceae, Pyrolaceae and Monotropaceae; Olacaceae and Santalaceae; Loranthaceae and Viscaceae; Convolvulaceae and Cuscutaceae; Lauraceae and Cassythaceae; Boraginaceae and Lennoaceae. In other cases it is due to the evolution of specialized pollination and dispersal mechanisms, e.g., Lythraceae and Punicaceae; Chenopodiaceae and Amaranthaceae; Ericaceae and Empetraceae; Campanulaceae and Lobeliaceae; Nymphaeaceae and Barclayaceae; and Solanaceae and Nolanaceae.

Thus, we anticipate significant changes in family circumscription as plant systematists develop more explicit genealogical hypotheses through phylogenetic analyses based on both molecular and morphological features. Some of these changes will involve uniting related paraphyletic and monophyletic family pairs (as discussed above). Others, however, will involve the splitting up of paraphyletic families, e.g., Flacourtiaceae, Phytolaccaceae, Liliaceae, Loganiceae, Saxifragaceae, and Simaroubaceae, as they are traditionally circumscribed (see Dahlgren, 1983; Dahlgren et al., 1985; Thorne, 1976, 1992a; Rodman, 1990; Bremer & Struwe, 1992).

Documentation of the phylogenetic pattern discussed here sets the stage for additional investigations. In a second paper (Donoghue, Judd, and Sanders, in prep.) we address the question of speciation rates in temperate and tropical family pairs. In particular, we consider why predominantly temperate lineages such as Brassicaceae, Apiaceae, and Lamiaceae are so speciose. We also relate our genealogical hypotheses to the paleobotanical and paleoclimatological records.

ACKNOWLEDGEMENTS

We thank the curators of the following herbaria for loans of selected specimens: A, FLAS, FTG, GH, LL, MO, NA, TEX, and US. We are grateful to Philip D. Cantino, Mary Fallen Endress, James Grimes, Kathleen A. Kron, Steven R. Manchester, Peter F. Stevens, Robert F. Thorne, Jack A. Wolfe, and Wendy B. Zomlefer for their helpful comments on the manuscript (or portions thereof), to Jennifer Chappill and Michael Sanderson for information on legume phylogeny, and to James E. Rodman for making available cladograms of glucosinolate taxa based on recent analyses of *rbc*L sequence data. We thank Dan Nicolson for his assistance in interpreting the International Code of Botanical Nomenclature. Michael Donoghue is grateful for support from the NSF (BSR-8822658), the University of Arizona, and a Mellon Foundation Fellowship from the Smithsonian Institution; W. Judd is grateful for support from the University of Florida; and R. Sanders is grateful for support from the Fairchild Tropical Garden. The results presented herein were briefly outlined in Sanders, Judd, and Donoghue (1991) and presented at the A.I.B.S. meetings in San Antonio; we thank numerous individuals who have offered suggestions and encouragement as a result of this (and other) oral presentations.

Walter S. Judd is primarily responsible for the phylogenetic analyses of Araliaceae and Apiaceae, Capparaceae and Brassicaceae, and Moraceae and Urticaceae; R. W. Sanders is primarily responsible for the analyses of Apocynaceae and Asclepiadaceae, and of Sapindaceae, Hippocastanaceae, and Aceraceae; and M. J. Donoghue is primarily responsible for the analysis of Caprifoliaceae, Dipsacaceae and Valerianaceae. Of course, each analysis has been modified as a result of suggestions made by the other authors as well as by other reviewers.

LITERATURE CITED

ABU-ASAB, M. S. 1990. Phylogenetic implications of pollen morphology in subfamily Lamioideae (Labiatae) and related taxa. Ph.D. Dissertation. Ohio University, Athens. Ohio.

——— & P. D. CANTINO. 1987. Pollen morphology of *Trichostema* (Labiatae) and its systematic implications. Syst. Bot. 14:359-369.

ADANSON, M. 1763. *Familles des plantes.* 2 vols. Paris: Vincent.

AIRY SHAW, H. K. 1932. Diagnoses of new families, new names, etc., for the seventh edition of Willis's 'Dictionary.' Kew Bull. 4:161-176.

AL-SHEHBAZ, I. A. 1973. The biosystematics of the genus *Thelypodium* (Cruciferae). Contr. Gray Herb. 204:3-148.

———. 1984. The tribes of Cruciferae (Brassicaceae) in the southeastern United States. J. Arnold Arbor. 65:343-373.

———. 1991. The genera of Boraginaceae in the southeastern United States. J. Arnold Arbor., supplementary series 1: 1-169.

ANDERBERG, A. A. 1992. The circumscription of the Ericales, and their cladistic relationships to other families of "higher" dicotyledons. Syst. Bot. 17: 660-675.

BAILEY, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. Amer. J. Bot. 31:421-428.

BAILLON, H. E. 1867-1895. *Histoire des plantes*. 13 vols. Paris: Gachette.

BAUMANN, M. G. 1946. *Myodocarpus* und die Phylogenie der Umbelliferen-Frücht. Ber. Schweiz. Bot. Ges. 56:13-112.

BAUMANN-BODENHEIM, M. G. 1955. Ableitung und Bau bicarpellat-monospermer und pseudomonocarpellater Araliaceen- und Umbelliferen-Früchte. Ber. Schweiz. Bot. Ges. 65:481-510.

BECHTEL, A. R. 1921. The floral anatomy of the Urticales. Amer. J. Bot. 8:386-410.

BEHNKE, H.-D. 1977. Dilatierte ER-Zisternen, ein mikromorphologisches Merkmal der Capparales? Ber. Deutsch. Bot. Ges. 90:241-251.

BENTHAM, G. & J. D. HOOKER. 1862. *Genera plantarum*. vol. 1. London: Lovell Reeve & Co.

BERG, C. C. 1977. Urticales, their differentiation and systematic position. Plant Syst. & Evol., Suppl. 1:349-374.

———. 1978. Cecropiaceae: a new family of the Urticales. Taxon 27:39-44.

———. 1989. Systematics and phylogeny of the Urticales. Pp. 193-220 in *Evolution, systematics, and fossil history of the Hamamelidae*, Vol. 2: *'Higher' Hamamelidae*, eds. P. R. Crane & S. Blackmore. Systematics Association Special Volume No. 40B. Oxford: Clarendon Press.

BESSEY, C. E. 1915. The phylogeny and taxonomy of flowering plants. Ann. Missouri Bot. Gard. 2:109-164.

BOHM, B. A. & C. W. M. GLENNIE. 1971. A chemosystematic study of the Caprifoliaceae. Canad. J. Bot. 49:1799-1807.

BOHNKE-GUTLEIN, E. & F. WEBERLING. 1981. Palynologische Untersuchungen an Caprifoliaceae. I. Sambuceae, Viburneae und Diervilleae. Trop. Subtrop. Pflanz. 34:131-189.

BONSEN, K. & B. J. H. TER WELLE. 1983. Comparative wood and leaf anatomy of the Cecropiaceae (Urticales). Bull. Mus. Nat. Hist. Nat. Paris, Sér. 4, 5 (sect. B, Adansonia, No. 2):151-177.

BREMER, B. & L. STRUWE. 1992. Phylogeny of the Rubiaceae and the Loganiaceae: congruence or conflict between morphological and molecular data? Amer. J. Bot. 79: 1171-1184.

BREMER, K. 1990. Combinable component consensus. Cladistics 6: 369-372.

——— & H.-E. Wanntorp. 1978. Phylogenetic systematics in botany. Taxon 27:317-329.

BROWN, R. 1818. Observations, systematical and geographical, on Professor Christian Smith's collection of plants from the vicinity of the river Congo. Pp. 420-488 in: J. K. Tuckey, *Narrative of an expedition to explore the river Zaire*. London: John Murray.

CANTINO, P. D. 1982. Affinities of the Lamiales: a cladistic analysis. Syst. Bot. 7: 237-248.

——— . 1990. The phylogenetic significance of stomata and trichomes in the Labiatae and Verbenaceae. J. Arnold Arb. 71:323-370.

———. 1992a. Evidence for a polyphyletic origin of the Labiatae. Ann. Missouri Bot. Gard. 79:361-379.

———. 1992b. Toward a phylogenetic classification of the Labiatae. Pp. 27-32 in *Advances in Labiate Science*, eds. R. M. Harley and T. Reynolds. Royal Bot. Garden, Kew.

———, R. M. Harley, and S. J. Wagstaff. 1992. Genera of Labiatae: status and classification. Pp. 511-522 in *Advances in Labiate Science*, eds. R. M. Harley and T. Reynolds. Royal Bot. Garden, Kew.

——— & R. W. Sanders. 1986. Subfamilial classification of Labiatae. Syst. Bot. 11:163-185.

CARLQUIST, S. 1981. Woody anatomy of Pittosporaceae. Allertonia 2: 355-392.

CHADWELL, T. B., S. J. WAGSTAFF, & P. D. CANTINO. 1992. Morphology of *Phryma* and some putative relatives. Syst. Bot. 17:210-219.

CHASE, M. W., D. E. SOLTIS, R. G. OLMSTEAD, D. MORGAN, D. H. LES, B. D. MISHLER, M. R. DUVALL, R. PRICE, H. G. HILLS, Y. QUI, K. A. KRON, J. H. RETTIG, E. CONTI, J. D. PALMER, J. R. MANHART, K. J. SYTSMA, H. J. MICHAELS, W. J. KRESS, K. G. KAROL, W. D. CLARK, M. HEDRÉN, B. S. GAUT, R. K. JANSEN, K. KIM, C. F. WIMPEE, J. F. SMITH,

G. R. FURNIER, S. H. STRAUSS, Q. XIANG, G. M. PLUNKETT, P. S. SOLTIS, S. M. SWENSEN, S. E. WILLIAMS, P. A. GADEK, C. J. QUINN, L. E. EGUIARTE, E. GOLENBERG, G. H. LEARN, JR., S. GRAHAM, S. C. H. BARRETT, S. DAYANANDAN, & V. A. ALBERT. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528-580.

CHERNIK, V. V. 1980. Peculiarities of structure and development of the pericarp of the representatives of the family Ulmaceae and Celtidaceae. Bot. Zhurn. (Leningrand and Moscow) 65:521-531. [in Russian]

CHEW, W.-L. 1963. Florae Malesiana precursor-XXXIV. A revision of the genus *Poikilospermum* (Urticaceae). Gardens' Bull. Singapore 20:1-103.

CONSTANCE, L. 1971. History of the classification of Umbelliferae (Apiaceae). Pp. 1-11 in *The biology and chemistry of the Umbelliferae*, ed., V. H. Heywood. London: Academic Press.

CORNER, E. J. H. 1962. The classification of Moraceae. Gardens' Bull. Singapore 19:187-252.

———. 1976. *The seeds of dicotyledons*, vols. 1 & 2. Cambridge: Cambridge University Press.

CRISP, M. D. & J. M. TAYLOR. 1990. A new species of *Bentleya* E. Bennett (Pittosporaceae) from southern Western Australia. J. Linn. Soc., Bot. 103: 309-315.

CRONQUIST, A. 1968. *The evolution and classification of flowering plants*. Boston: Houghton Mifflin Company.

———. 1981. *An integrated system of classification of flowering plants*. New York: Columbia University Press.

———. 1988. *The evolution and classification of flowering plants*. Ed. 2. New York: The New York Botanical Garden.

CUELLAR, H. S. 1967. Description of a pollen release mechanism in the flower of the Mexican hackberry tree, *Celtis laevigata*. Southwestern Naturalist 12:471-474.

DAHL, A. 1990. Infrageneric division of the genus *Hypecoum* (Papaveraceae). Nord. J. Bot. 10: 129-140.

DAHLGREN, G. 1989. The last Dahlgrenogram. System of classification of the dicotyledons. Pp. 249-260 in *The Davis and Hedge Festschrift*, ed. K. Tan. Edinburgh: University Press.

DAHLGREN, R. 1975. A system of classification of the Angiosperms to be used to demonstrate the distribution of characters. Bot. Notis. 128: 119-147.

———. 1980. A revised system of classification of the angiosperms. Bot. J. Linnean Soc. 80:91-124.

———. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3:119-149.

———, H. T. CLIFFORD, & P. F. YEO. 1985. *The families of the Monocotyledons*. Berlin: Springer-Verlag.

DE QUEIROZ, K. & J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39:307-322.

——— & ——— 1992.Phylogenetic taxonomy. Ann. Rev. Ecol. Syst. 23: 449-480.

DEVOS, F. 1951. The stem anatomy of some species of the Caprifoliaceae with reference to phylogeny and identification of the species. Ph.D. dissertation, Cornell Univ., Ithaca, NY.

DEWOLF, G. P. 1962. Notes on African Capparidaceae: III. Kew Bull. 16:75-83.

DICKISON, W. C. 1975. The bases of angiosperm phylogeny: vegetative anatomy. Ann. Missouri Bot. Gard. 62:590-620.

———. 1986. Wood anatomy and affinities of the Alseuosmiaceae. Syst. Bot. 11:214-221.

DONOGHUE, M. J. 1983. The phylogenetic relationships of *Viburnum*. Pp. 143-166 in *Advances in Cladistics*, Vol. 2, eds. N. I. Platnick and V. A. Funk. New York: Columbia University Press.

———. 1985. Pollen diversity and exine evolution in *Viburnum* and the Caprifoliaceae *sensu lato*. J. Arnold Arbor. 66:421-469.

——— & P. D. Cantino. 1988. Paraphyly, ancestors, and the goals of taxonomy: A botanical defense of cladism. Bot. Rev. 54:107-128.

———, R. G. OLMSTEAD, J. F. SMITH, & J. D. PALMER. 1992. Phylogenetic relationships of Dipsacales based on *rbc*L sequences. Ann. Missouri Bot. Gard. 79:333-345.

DOWNIE, S. R. & J. D. PALMER. 1992. Restriction site mapping of the chloroplast DNA inverted repeat: A molecular phylogeny of the Asteridae. Ann. Missouri Bot. Gard. 79:266-283.

DVORÁK, F. 1973. The importance of the indumentum for the investigation of evolutional relationship in the family Brassicaceae. Österr. Bot. Zeitschr. 121:155-164.

EAMES, A. J. & C. L. WILSON. 1928. Carpel morphology in the Cruciferae. Amer. J. Bot. 15:251-270.

EDLIN, H. L. 1935. A critical revision of certain taxonomic groups of the Malvales. New Phytol. 34:1-20, 122-143.

EICHLER, A. W. 1875-1878. *Blüthendiagramme, construirt und erläutert*. 2 vols. Leipzig.

EL-GAZZAR, A. & L. WATSON. 1970. A taxonomic study of Labiatae and related genera. New Phytol. 69:451-486.

ELIAS, T. S. 1970. The genera of Ulmaceae in the southeastern United States. J. Arnold Arbor. 51:18-40.

ENDRESS, P. K., M. JENNY, & M. E. FALLEN. 1983. Convergent elaboration of apocarpous gynoecia in higher advanced dicotyledons (Sapindales, Malvales, Gentianales). Nordic J. Bot. 3:293-300.

ENGLER, H. G. A. 1889. Ulmaceae, Moraceae, and Urticaceae. Die natürlichen Pflanzenfamilien 3(1):59-118.

ERBAR, C. 1991. Sympetalae -- a systematic character? Bot. Jahrb. Syst. 112:417-451.

——— & P. LEINS. 1988. Blutenentwicklungsgeschichtliche Studies an *Aralia* und *Hedera* (Araliaceae). Flora 180:391-406.

ERDTMAN, G. 1945. Pollen morphology and plant taxonomy. IV. Svensk. Bot. Tidskr. 39:279-285.

———. 1971. *Pollen morphology and plant taxonomy*. New York: Hafner.

ERNST, W. R. 1962. The genera of Papaveraceae and Fumariaceae in the southeastern United States. J. Arnold Arbor. 43:315-343.

———. 1963. The genera of Capparaceae and Moringaceae in the southeastern United States. J. Arnold Arbor. 44:81-95.

ETTLINGER, M. G. & A. KJAER. 1968. Sulfur compounds in plants. Pp. 59-144 in *Recent advances in phytochemistry*. Vol. 1., eds. T. J. Mabry, R. E. Alston, & V. C. Runeckles. New York: Appleton-Century-Crofts.

EYDE, R. H. & C. C. TSENG. 1969. Flower of *Tetraplasandra gymnocarpa*: hypogyny with epigynous ancestry. Science 166:506-508.

——— & C. C. TSENG. 1971. What is the primitive floral structure of Araliaceae? J. Arnold Arbor. 52:205-239.

FALLEN, M. E. 1986. Floral strucure in the Apocynaceae: Morphological, functional, and evolutionary aspects. Bot. Jahrb. Syst. 106:245-286.

FARRIS, J. S. 1982. Outgroups and parsimony. Syst. Zool. 31: 328-334.

FRIIS, I. 1989. The Urticaceae: a systematic review. Pp. 285-308. in *Evolution, systematics, and fossil history of the Hamamelidae*, Vol. 2: *'Higher' Hamamelidae*, eds. P. R. Crane & S. Blackmore. Systematics Association Special Volume No. 40B. Oxford: Clarendon Press.

FRITSCH, K. 1891. Caprifoliaceae. Die natürlichen Pflanzenfamilien 4(4):159-169.

FUKUOKA, N. 1972. Taxonomic study of the Caprifoliaceae. Mem. Fac. Sci. Kyoto Univ. Ser. Biol. 6:15-58.

GARDNER, R. O. 1978. Systematic notes on the Alseuosmiaceae. Blumea 24:138-142.

GIANNASI, D. E. 1978. Generic relationships in the Ulmaceae based on flavonoid chemistry. Taxon 27:331-344.

GIBBS, R. D. 1974. *Chemotaxonomy of flowering plants.* Vol. 3. Montreal: McGill-Queen's University Press.

GIBSON, A. C. 1979. Anatomy of *Koeberlinia* and *Canotia* revisited. Madroño 26:1-12.

GRAHAM, S. A. 1966. The genera of Araliaceae in the southeastern United States. J. Arnold Arbor. 47:126-136.

GREUTER, W., ed. 1988. *International Code of Botanical Nomenclature*. Konigstein, Germany: Koeltz Scientific Books.

GRUDZINSKAJA, I. A. 1967. Ulmaceae and reasons for distinguishing Celtidoideae as a separate family Celtidaceae Link. Bot. Zhurn. (Leningrad) 52 (12):1723-1749. [in Russian].

HALLIER, H. 1903. Über die Verwandtschaftsverhältnisse bei Engler's Rosalen, Parietalen, Myrtifloren und in anderen Ordnungen der Dikotylen. Abh. Naturw. Hamburg 18:3-98.

———. 1905. Provisional scheme of the natural (phylogenetic) system of flowering plants. New Phytol. 4:151-162.

———. 1912. L'origine et le système phylétique des Angiosperms exposés à l'aide de leur arbre généalogique. Arch. Néerl. Sci. Exact. Nat. Ser. 3, 1:146-234.

HARA, H. 1983. *A revision of the Caprifoliaceae of Japan with reference to allied plants in other districts and the Adoxaceae*. Tokyo: Academia Scientific Books.

HAUSER, L. A. & T. J. CROVELLO. 1982. Numerical analysis of generic relationships in Thelypodieae (Brassicaceae). Syst. Bot. 7:249-268.

HEGNAUER, R. 1969. Chemical evidence for the classification of some plant taxa. Pp. 121-138 in *Perspectives in phytochemistry*, eds., J. B. Harborne and T. Swain. London: Academic Press.

———. 1971. Chemical patterns and relationships of Umbelliferae. Pp. 267-277 in *The biology and chemistry of the Umbelliferae*, ed., V. H. Heywood. London: Academic Press.

HEIMSCH, C. 1942. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales" of Wettstein, with reference to taxonomic grouping. Lilloa 8: 83-198.

HENDY, M. D. & D. PENNY. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosci. 59:277-290.

HICKEY, L. J. & J. A. WOLFE. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62:538-589.

HOFMANN, U. & J. GOTTMANN. 1990. *Morina* L. and *Triplostegia* Wall ex DC. im Vergleich mit Valerianaceae und Dipsacaceae. Bot. Jahrb. 111:499-553.

HUFFORD, L. 1992. Rosidae and their relationships to other nonmagnoliid dicotyledons: A phylogenetic analysis using morphological and chemical data. Ann. Missouri Bot. Gard. 79:218-248.

HUMPHRIES, C. J. & S. BLACKMORE. 1989. A review of the classification of the Moraceae. Pp. 267-277 in *Evolution, systematics, and fossil history of the Hamamelidae*, Vol. 2: *'Higher' Hamamelidae*, eds. P. R. Crane & S. Blackmore. Systematics Association Special Volume No. 40B. Oxford: Clarendon Press.

HUTCHINSON, J. 1926. *The families of flowering plants*. London: Macmillan and Company, Ltd.

——— 1969. *Evolution and phylogeny of flowering plants*. London: Academic Press.

———. 1973. *The families of flowering plants*. Oxford: Clarendon Press.

ILTIS, H. H. 1957. Studies in the Capparidaceae. III. Evolution and phylogeny of the western north American Cleomoideae. Ann. Missouri Bot. Gard. 44:77-119.

———. 1958. Studies in the Capparidaceae. IV. *Polanisia* Raf. Brittonia 10:33-58.

———. 1959. Studies in the Capparidaceae. VI. *Cleome* sect. *Physostemon*: taxonomy, geography and evolution. Brittonia 11:123-162.

IVERSEN, T.-H. 1970. The morphology, occurrence, and distribution of dilated cisternae of the endoplasmic reticulum in tissues and plants of the Cruciferae. Protoplasma 71:467-477.

JACKSON, G. A. 1933. A study of the carpophore of the Umbelliferae. Amer. J. Bot. 20:121-144.

JANCHEN, E. 1942. Das System der Cruciferen. Österr. Bot. Zeitschr. 91:1-28.

JAY, M. 1969. Chemotaxonomic researches on vascular plants XIX. Flavonoid distribution in the Pittosporaceae. J. Linn. Soc., Bot. 62: 423-429.

JOHNSTON, I. M. 1950. Studies in the Boraginaceae, XIX. J. Arnold Arbor. 31: 172-195.

JORGENSEN, L. B. 1981. Myrosin cells and dilated cisternae of the endoplasmic reticulum in the order Capparales. Nordic. J. Bot. 1:433-445.

JUNELL, S. 1934. Zur Gynaceummorphologie und Systematik der Verbenaceen und Labiaten. Symb. Bot. Upsal. 4:1-219.

KUNZE, H. 1982. Morphogenese und Synorganisation des Bestäubungfsapparates einiger Asclepiadaceen. Beitr. Biol. Pflanzen 56:133-170.

LAVIN, M., J. J. DOYLE & J. D. PALMER. 1990. Evolutionary significance of the loss of the chloroplast-DNA inverted repeat in the Leguminosae subfamily Papilionoideae. Evolution 44:390-402.

LAWRENCE, G. H. M. 1951. Taxonomy of vascular plants. New York: The Macmillan Company.

LI, H.-L. 1942. The Araliaceae of China. Sargentia 2:1-134.

LIDÉN, M. 1986. Synopsis of Fumarioideae (Papaveraceae) with a monograph of the tribe Fumarieae. Opera Bot. 88. 5-129.

LISTON, A. 1992. Use of the polymerase chain reaction to survey for the loss of the inverted repeat in the legume chloroplast genome. P. 20, Abstracts. Third International Legume Conference, Royal Botanic Gardens, Kew.

MACFARLANE, J. M. 1933. *The evolution and distribution of flowering plants*. Vol. I. *The Apocynaceae and Asclepiadaceae*. Philadelphia: Noel Printing Company.

MADDISON, W. P. & D. R. MADDISON. 1992. *MacClade: Interactive analysis of phylogeny and character evolution, Version 3.0.* Sunderland, Massachusetts: Sinauer Assoc.

———, M. J. DONOGHUE, & D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83-103.

MAHESHWARI, P. 1946. The *Adoxa* type embryo sac: a critical review. Lloydia 9:73-113.

MANCHESTER, S. R. 1992. Flowers, fruits, and pollen of *Florissantia*, an extinct malvalean genus from the Eocene and Oligocene of western North America. Amer. J. Bot. 79: 996-1008.

MAYR, E. 1969. *Principles of systematic zoology*. New York: McGraw-Hill Book Co.

MCVAUGH, R. 1943. The genus *Triodanis* Rafinesque, and its relationships to *Specularia* and *Campanula*. Wrightia 1: 13-52.

MEEUSE, A. D. J. 1975. Taxonomic relationships of Salicaceae and Flacourtiaceae: their bearing on interpretative floral morphology and dilleniid phylogeny. Acta Bot. Neerl. 24:437-457.

MELCHIOR, H. 1964. *Engler's Syllabus der Pflanzenfamilien,* ed 12, vol 2. Gebrüder Borntraeger.

METCALFE, C. R. 1966. Distribution of latex in the plant kingdom. Notes from the Jodrell Laboratory 3:1-18.

——— & L. CHALK. 1950. Urticaceae, Pp. 1244-1254. *Anatomy of the Dicotyledons,* vol. 2. Oxford: Clarendon Press.

MILLER, N. G. 1971. The genera of the Urticaceae in the southeastern United States. J. Arnold Arbor. 52:40-68.

MISHLER, B. D. & R. N. BRANDON. 1987. Individuality, pluralism, and the phylogenetic species concept. Biology and Philosophy 2:397-414.

MULLER, J., & P. W. LEENHOUTS. 1976. A general survey of pollen types in Sapindaceae in relation to taxonomy. Pp. 407-445 in *The evolutionary significance of the exine*, eds. I. K. Ferguson and J. Muller. London: Academic Press.

NIXON, K. C. & J. I. DAVIS. 1991. Polymorphic taxa, missing values and cladistic analysis. Cladistics 7:233-241.

OGINUMA, K., P. H. RAVEN, & H. TOBE. 1990. Karyomorphology and relationships of Celtidaceae and Ulmaceae (Urticales). Bot. Mag. Tokyo 103:113-131.

OLMSTEAD, R. G., H. J. MICHAELS, K. M. SCOTT, & J. D. PALMER. 1992. Monophyly of the Asteridae and identification of its major lineages inferred from *rbc*L sequences. Ann. Missouri Bot. Gard. 79:249-265.

———, B. BREMER, K. M. SCOTT, & J. D. PALMER. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbc*L sequences. Ann. Missouri Bot. Gard. 80: 700-722.

PAX, F. 1891a. Tovariaceae. Pp. 207-208 in *Die natürlichen Pflanzenfamilien* vol. 3(2), eds. A. Engler & K. Prantl. Leipzig: Wilhelm Engelmann.

———. 1891b. Capparidaceae. Pp. 209-236 in *Die natürlichen Pflanzenfamilien* vol. 3(2), eds. A. Engler & K. Prantl. Leipzig: Wilhelm Engelmann.

PAYSON, E. B. 1923. A monographic study of the genus *Thelypodium* and its immediate allies. Ann. Missouri Bot. Gard. 9:233-324.

PLUNKETT, G. M., D. E. SOLTIS, & P. S. SOLTIS. 1992. Molecular phylogenetic study of Apiales (Apiaceae, Araliaceae, and Pittosporaceae). Amer. J. Bot. 79(6, part 2):158.

POLHILL, R. M. 1981. Papilionoideae. Pp. 191-208 in *Advances in Legume Systematics*, Part 1, eds., R. M. Polhill and P. H. Raven. Royal Botanic Garden, Kew.

——— & P. H. Raven (eds.). 1981. *Advances in Legume Systematics, Part 1*. Royal Botanic Garden, Kew.

PURI, V. 1950. Studies in floral anatomy. VI. Vascular anatomy of the flower of *Crateva religiosa* Forst., with special reference to the nature of the carpels in the Capparidaceae. Amer. J. Bot. 37:363-370.

———. 1951. The role of floral anatomy in the solution of morphological problems. Bot. Rev. 17:471-553.

RADLKOFER, L. 1890. Uber die Gliederung der Familie der Sapindaceen. Sitzungsber. Math.-Phys. Kl. Bayer. Akad. Wiss. München. 20:105-379.

———. 1895. Sapindaceae. Pp. 277-326, 460-462 in *Die natürlichen Pflanzenfamilien* vol. 3(5), eds. A. Engler & K. Prantl. Leipzig: Wilhelm Engelmann.

REHDER, A. 1935. *Handeliodendron*, a new genus of Sapindaceae. J. Arnold Arbor. 16:65-68.

ROBSON, N. K. B. 1977. Studies in the genus *Hypericum* L. (Guttiferae). I. Infrageneric classification. Bull. British Mus. (Nat. Hist.) Bot. 5:293-355.

RODMAN, J. E. 1981. Divergence, convergence, and parallelism in phytochemical characters: The glucosinolate-myrosinase system. Pp. 43-79 in *Phytochemistry and angiosperm phylogeny*, eds. D. A. Young and D. S. Seigler. New York: Praeger.

———. 1990. Centrospermae revisited, part I. Taxon 39:383-393.

———. 1991a. A taxonomic analysis of glucosinolate-producing plants, part 1: Phenetics. Syst. Bot. 16:598-618.

———. 1991b. A taxonomic analysis of glucosinolate-producing plants, part 2: Cladistics. Syst. Bot. 16:619-629.

———, R. PRICE, K. KAROL, E. CONTI, K. SYTSMA, & J. PALMER. 1992. Gene sequence evidence for monophyly of mustard oil plants. Amer. J. Bot. 79:160, 161.

———, R. PRICE, K. KAROL, E. CONTI, K. SYTSMA, & J. PALMER. 1993. Nucleotide sequences of the *rbc*L gene indicate monophyly of mustard oil plants. Ann. Missouri Bot. Gard. 80: 686-699.

RODRÍGUEZ, R. L. 1957. Systematic anatomical studies on *Myrrhidendron* and other woody Umbellales. Univ. Calif. Publ. Bot. 29:145-318.

———. 1971. The relationships of the Umbellales. Pp. 63-91 in *The biology and chemistry of the Umbelliferae*, ed., V. H. Heywood. London: Academic Press.

ROGERS, C. L. 1950. The Umbelliferae of North Carolina and their distribution in the southeast. J. Elisha Mitchell Sci. Soc. 66:195-266.

ROLLINS, R. C. 1956. Some new primitive Mexican Cruciferae. Rhodora 58:148-157.

ROSATTI, T. J. 1989. The genera of suborder Apocynineae (Apocynaceae and Asclepiadaceae) in the southeastern United States. J. Arnold Arbor. 70:307-401.

SAFWAT, F. 1962. The floral morphology of *Secamone* and the evolution of the pollinating apparatus in Asclepiadaceae. Ann. Missouri Bot. Gard. 49:95-129.

SANDERS, R. W., W. S. JUDD, & M. J. DONOGHUE. 1991. Do the temperate-tropical family pairs constitute sister groups? Amer. J. Bot. 78: 213, 214.

SAX, K. & D. A. KRIBS. 1930. Chromosomes and phylogeny in Caprifoliaceae. J. Arnold Arbor. 11:147-153.

SCHICK, B. 1980. Untersuchungen über die Biotechnik der Apocynaceenblüte. I. Morphologie und Funktion des Narbenkopfes. Flora 170:394-432.

———. 1982. Untersuchungen über die Biotechnik der Apocynaceenblüte. II. Bau und Funktion des Bestaubungsapparates. Flora 172:347-371.

SCHUMANN, K. 1895. Asclepiadaceae. Pp. 189-306 in *Die natürlichen Pflanzenfamilien,* vol. 4(2), eds. A. Engler & K. Prantl. Leipzig: Wilhelm Engelmann.

SOLEREDER, H. 1895. Loganiaceae. Pp. 19-50 in *Die natürlichen Pflanzenfamilien* 4(2), eds. A. Engler & K. Prantl. Leipzig: Wilhelm Engelmann.

STÅHL, B. 1990. Taxonomic studies in the Theophrastaceae. Dissertation. Göteborg, Sweden: Department of Systematic Botany, University of Göteborg.

STEBBINS, G. L. 1974. *Flowering plants: evolution above the species level*. Cambridge, Massachusetts: Belknap Press.

STEENIS, C. G. G. J. VAN. 1984. A synopsis of Alseuosmiaceae in New Zealand, New Caledonia, Australia, and New Guinea. Blumea 29:387-394.

STEVENS, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Syst. 11:333-358.

———. 1988. On the phylogeny of the Bonnetiaceae-Hypericaceae-Clusiaceae, or the consequences of putting water in a rocket engine. Amer. J. Bot. 75(6, part 2): 209.

———. 1991. Character states, morphological variation, and phylogenetic analysis: a review. Syst. Bot. 16:553-583.

———. 1994. *The development of biological systematics.* Columbia Univ. Press. (in press).

SWOFFORD, D. L. 1991. *PAUP: Phylogenetic analysis using parsimony, Version 3.0*. Champaign, Illinois: Illinois Natural History Survey.

TAKHTAJAN, A. L. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46:225-359.

———. 1987. *Sistema Magnoliofitov*. Acad. Sciences USSR, Leningrad.

TERABAYASHI, S. 1991. Vernation patterns in Celtidaceae and Ulmaceae (Urticales), and their evolutionary and systematic implications. Bot. Mag. Tokyo 104:1-13.

THORNE, R. F. 1973a. Inclusion of the Apiaceae (Umbelliferae) in the Araliaceae. Notes Royal Bot. Gard. Edinburgh 32:161-165.

———. 1973b. The 'Amentiferae' or Hamamelidae as an artificial group: a summary statement. Brittonia 25:395-405.

———. 1974. A phylogenetic classification of the Annoniflorae. Aliso 8:147-209.

———. 1976. A phylogenetic classification of the Angiospermae. Evolutionary Biology 9:35-106.

———. 1981. Phytochemistry and Angiosperm phylogeny: a summary statement. Pp. 233-295 in *Phytochemistry and Angiosperm Phylogeny,* eds. D. A. Young and D. S. Seigler. New York: Praeger.

———. 1983. Proposed new realignments in the angiosperms. Nordic J. Bot. 3:85-117.

———. 1992a. An updated phylogenetic classification of the flowering plants. Aliso 13:365-389.

———. 1992b. Classification and geography of the flowering plants. Bot. Rev. 58: 225-348.

TIPPO, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. Bot. Gaz. 100:1-99.

TROLL, W. & F. WEBERLING. 1966. Die Infloreszenzen der Caprifoliaceen und ihre systematische Bedeutung. Abh. Math.-naturwiss. Klasse. Akad. Wiss. Lit. Mainz 1966:455-605.

Tucker, C. T., A. W. Douglas, & L. Han-Xing. 1993. Utility of ontogenetic and conventional characters in determining phylogenetic relationships of Saururaceae and Piperaceae. Syst. Bot. 18: 614-641.

Umadevi, I. & M. Daniel. 1991. Chemosystematics of the Sapindaceae. Feddes Repert. 102:607-612.

Van der Pijl, L. 1957. On the arilloids of *Nephelium*, *Euphoria*, *Litchi* and *Aesculus*, and the seeds of Sapindaceae in general. Acta Bot. Neerl. 6:618-641.

Van Tieghem, P. 1884. Sur la structure et les affinités des Pittosporées. Bull. Soc. Bot. Fr. 31: 384-385.

Vaughan, J. G. & J. M. Whitehouse. 1971. Seed structure and the taxonomy of the Cruciferae. J. Linn. Soc., Bot. 64:383-409.

Wagenitz, G. 1992. The Asteridae: evolution of a concept and its present status. Ann. Missouri Bot. Gard. 79: 209-217.

——— & B. Laing. 1984. Die Nektarien der Dipsacales und ihre systematische Bedeutung. Bot. Jarb. Syst. 104:91-113.

Walters, S. M. 1961. The shaping of angiosperm taxonomy. New Phytol. 60: 74-84.

Wanntorp, H.-E. 1988. The genus *Microloma* (Asclepiadaceae). Opera Bot. 98:1-69.

Weberling, F. 1957. Morphologische Untersuchungen zur Systematik der Caprifoliaceen. Abhandlungen der Math.- naturwiss. Klasse. Akad. Wiss. Lit. Mainz 1957:1-50.

———. 1989. *Morphology of flowers and inflorescences.* Cambridge: Cambridge University Press.

——— & M. Hildenbrand. 1986. Weitere Untersuchungen zur Tapetumentwicklung der Caprifoliaceae. Beitr. Biol. Pfl. 61:3-20.

Weddell, H. A. 1856-7. Monographie de la famille des Urticées. Arch. Mus. Hist. Nat. Paris 19:1-519.

Wilkinson, A. M. 1949. Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. Amer. J. Bot. 36:481-489.

Wolfe, J. A., & T. Tanai. 1987. Systematics, phylogeny, and distribution of *Acer* (Maples) in the Cenozoic of western North America. J. Fac. Sci., Hokkaido Univ. 22:1-246.

——— & W. Wehr. 1987. *Middle Eocene dicotyledonous plants from Republic, northeastern Washington.* Denver: U.S Geological Survey Bull. 1597.

Wood, C. E. & P. Adams. 1976. The genera of Guttiferae (Clusiaceae) in the southeastern United States. J. Arnold Arbor. 57:74-90.

Yamazaki, T. 1974. A system of Gamopetalae based on embryology. J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 11:263-281.

Note added in proof:

Recent cladistic analyses of *rbc*L sequence data have suggested that, among other, the Caesalpiniaceae (Ballenger et al., 1993), Simaroubaceae (Gadek et al., 1993), Scrophulariaceae (Reeves & Olmstead, 1993), and Ericaceae (Kron & Chase, 1993) are paraphyletic. Recently published morphological analyses also support the paraphyly of the Ericaceae (Anderberg, 1933; Judd & Kron, 1993). See references cited below:

Anderberg, A. A. 1993. Cladistic interrelationships and major clades of the Ericales. Pl. Syst. Evol. 184: 207-231.

Ballenger, J. A., E. Dickson, M. Meyer, & J. J. Doyle. 1993. DNA sequence data and the phylogeny of the Leguminosae. Amer. J. Bot. (6, part 2): 130, 131.

Gadek, P. A., E. S. Fernando, D. M. Crayn, & C. J. Quinn. 1993. Molecular systematics of Simaroubaceae *sensu lato*. Amer. J. Bot. 80 (6, part 2); 149, 150.

Judd, W. S. & K. A. Kron. 1993. Circumscription of Ericaceae (Ericales) as determined by pre-liminary cladistic analyses based on morphological, anatomical, and embryological features. Brittonia 45: 99-114.

Kron, K. A. & M. W. Chase. 1993. Systematics of the Ericaceae, Empetraceae, Epacridaceae and related taxa based upon *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 735-741.

Reeves, P. A. & R. G. Olmstead. 1993. Polyphyly of the Scrophulariaceae and origin of the aquatic Callitrichaceae inferred from chloroplast DNA sequences. Amer. J. Bot. 80 (6, part 2): 174.